

Myctophid Feeding Ecology and Carbon Transport along the Northern Mid-Atlantic
Ridge

A Thesis

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The Faculty of the School of Marine Science
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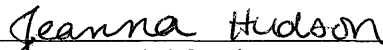
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APPROVAL SHEET

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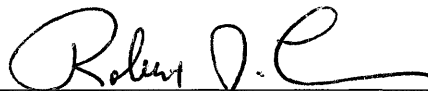


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ABSTRACT

The Mid-Atlantic Ridge (MAR) is the largest topographic feature in the Atlantic Ocean, yet little is known about the food web structure and trophic ecology of fishes inhabiting mesopelagic waters along the MAR. To better understand the food web structure and to compare the feeding ecology of abundant MAR fishes to those in off-ridge areas, MAR-ECO, a Mid-Atlantic Ridge ecosystem field project of the Census of Marine Life, sampled the pelagic fauna of the northern MAR (Iceland to the Azores) during June-July, 2004. Samples were collected with two midwater trawls outfitted with multiple opening and closing cod ends to sample discrete depths from the surface to >2300 m at predefined stations within four ridge sections. Fishes of the family Myctophidae were the most abundant fishes collected, with the myctophid *Benthosema glaciale* the numerically dominant species. The feeding ecology of three myctophid species, *B. glaciale*, *Protomyctophum arcticum*, and *Hygophum hygomii*, were quantified through dietary analysis. Each species was predominantly zooplanktivorous, consuming copepods, euphausiids, ostracods, and other crustacean zooplankton, with each myctophid species exhibiting unique dietary patterns. Different abiotic parameters influenced variability in the diet of *B. glaciale* and *P. arcticum* as determined by canonical correspondence analysis. Of the measured parameters, ridge section and time of day were significant explanatory variables in the diet of *B. glaciale*, while only depth was significant in the diet of *P. arcticum*. Daily consumption by *B. glaciale* and *P. arcticum* was highest at the Reykjanes Ridge and Charlie-Gibbs Fracture Zone, respectively; consumption by *H. hygomii* was only measured at the Azorean Zone. Daily consumption of all three species was less than 1% of dry body weight. Active transport

of carbon out of the euphotic zone by diel vertically migrating MAR myctophids through respiration of CO₂, excretion of dissolved organic carbon, and egestion of particulate organic carbon (POC) was also estimated, and compared to passive sinking of POC in the North Atlantic. Active carbon flux by the 0-200 m integrated migrant myctophid biomass, uncorrected for trawl efficiency, ranged from 0.01-0.4% of sinking POC flux at 150 m and 0.02-0.95% at 300 m. If myctophid biomass was corrected for low gear efficiency, flux increased to 0.1-1% and 0.3-3.5%, respectively, of sinking POC. Lower MAR myctophid biomass resulted in lower active carbon transport compared to myctophids in the Pacific and zooplankton in the North Atlantic estimated in previous studies, but myctophid active transport should still be considered in models of MAR carbon cycling. Due to the role of myctophids as both predators of numerous zooplankton taxa and as prey of higher taxa, information on the feeding ecology and daily consumption of these fishes is necessary to accurately assess their role in the MAR food web and the overall trophic structure of this hydrodynamically and topographically unique ecosystem.

Myctophid Feeding Ecology and Carbon Transport along the Northern Mid-Atlantic
Ridge

INTRODUCTION

Fishes of the family Myctophidae are an integral part of the trophodynamics of oceanic ecosystems around the world, including the North Atlantic Ocean. The diets of myctophids are probably most well known from the eastern and western sides of the North Atlantic Ocean; however, the feeding ecology and role in carbon cycling of myctophids associated with the northern Mid-Atlantic Ridge (MAR), part of the largest topographic feature in the Atlantic Ocean, is completely unknown. The purpose of this thesis is to compare the feeding ecology of, and carbon export by, myctophids at the MAR to myctophids in off-ridge areas of the North Atlantic and other ocean basins.

Myctophid ecology and potential role in carbon export

Fishes of the family Myctophidae are distributed globally and reside from the surface to depths greater than 1000 m. They are the most numerically abundant mesopelagic fish family in many areas around the world (Frost and McCrone 1979, Balanov and Il'inskii 1992, Beamish et al. 1999, Sutton et al. 2008). Information on the feeding ecology and trophic position of these fishes is critical to the understanding of ecosystem food webs and modeling of large-scale ecological processes in the ocean.

Myctophids generally occupy a tertiary trophic level, feeding primarily on crustacean zooplankton, but they are also known to feed on gelatinous zooplankton, pteropods, and other non-crustacean prey including other fishes (Kinzer 1982, Sameoto 1988, Hopkins et al. 1996, Moku et al. 2000). Hopkins et al. (1996) found that myctophids were the most important consumer in a Gulf of Mexico assemblage consisting of 164 species representing 16 families of midwater fishes, ingesting 31% of

the total prey biomass consumed daily by the assemblage. In the eastern Gulf of Mexico, a low-latitude myctophid community consumed 8-16% of the total copepod daily production and 2% of the overall zooplankton biomass each night (Hopkins and Gartner 1992). Gorelova (1984) estimated that myctophids may consume 2-31% (average 10%) of the zooplankton standing stock daily in the equatorial Pacific. A wide range of daily consumption has been estimated for myctophids, generally falling within 1-6% of body weight for adults (Sameoto 1988, Pahkomov et al. 1996, Brodeur and Yamamura 2005).

While myctophids are important predators, they are also important prey for higher order predators such as marine mammals, sea birds, and piscivorous fishes (Hopkins et al. 1996, Beamish et al. 1999, Pusineri et al. 2008, Pereira et al. 2011). The diet of stomiid fishes in a Gulf of Mexico assemblage was comprised mainly of fishes (83% of abundance), of which myctophids represented 42% (Hopkins et al. 1996). Myctophids have also been identified in the diets of swordfish, albacore tuna, common dolphin, striped dolphin and beaked whales, constituting as much as 50% of the diet by mass (Pusineri et al. 2008, Pereira et al. 2011). Beamish et al. (1999) postulated that myctophids may constitute up to 90% of the diets of northern fur seal, Dall's Porpoise, Pacific white-sided dolphin, and northern right whale dolphin in the subarctic Pacific. Additionally, myctophids were a notable component of the diet of many sea birds in this area, including several species of puffins, murre, and kittiwakes (Beamish et al. 1999).

Many myctophid species make daily vertical migrations up to the epipelagic zone at night to feed on zooplankton, and migrate to deeper water (~300-1000 m) during the day where they digest their food. While metabolizing this surface-derived food at depth, myctophids egest large, fast-sinking, carbon-rich fecal pellets, respire carbon dioxide, and

excrete dissolved organic carbon and dissolved organic and inorganic nitrogen. This “active transport” of organic and inorganic nutrients may be an important component of the biological pump (collectively the vertical export of surface-derived nutrients to depth by vertically migrating zooplankton and fishes, ‘passive’ sinking of dead phytoplankton aggregates and of fecal pellets, and physical mixing of dissolved organic matter) and subsidizes the metabolic demands of deep-sea organisms in an extremely food-limited environment (Vinogradov 1962, Steinberg et al. 2000, 2008, Hidaka et al. 2001, Wotton and Malmqvist 2001). Hidaka et al. (2001) found the respiratory flux due to vertically migrating micronekton in the western equatorial Pacific (biomass corrected for assumed gear sampling efficiency of 14%) to be between 15-30 mg C m⁻² d⁻¹, which accounted for 28-55% of the sinking particulate organic carbon (POC) flux, while the gut flux (material consumed near the surface that is egested as fecal pellets at depth) accounted for 2-3% of POC flux. Respiratory and gut fluxes due to migrant myctophids accounted for approximately 14-26% and 1-2%, respectively, of the POC flux. In addition, Wilson et al. (2009) reported that carbonate production within the intestines of marine fishes, which is released via excretion, contributes 3-15% of total oceanic carbonate production. Given that myctophids are the dominant group of vertically migrating fishes and account for the greatest proportion of fish biomass in the epipelagic zone at night (Maynard et al. 1975, Hopkins and Lancraft 1984), myctophids have the potential to export a significant amount of organic and inorganic carbon to the deep sea.

The Mid-Atlantic Ridge and the MAR-ECO study

The continental slope regions of the ocean make up a small proportion of the earth's surface area (Garrison 2010). Beyond the narrow continental slope, organisms in the mesopelagic zone rarely encounter land. The high pressures and cold temperatures prevent most mesopelagic organisms from reaching the sea floor, except at seamounts and mid-ocean ridges. Mid-ocean ridges, abrupt, hard-bottomed topographic features that stretch 65,000 km around the world (Garrison 2010), protrude up into the water column to create relatively shallow, diverse habitat structure in an otherwise structurally homogeneous medium. In the Atlantic Ocean the Mid-Atlantic Ridge (MAR) divides the ocean into nearly equal eastern and western halves. It provides a unique, relatively shallow habitat in the center of the deep Atlantic Ocean and supports a diverse faunal assemblage (Vecchione et al. 2010). The MAR exhibits many unique topographical features including the Charlie-Gibbs Fracture Zone, where deep sub-marine rift valleys run east to west and influence local and regional circulation patterns. Such alterations in circulation patterns may affect the distribution and feeding ecology of deep-sea organisms including those that inhabit the ridge as well as transient (migratory) species (Roden 1987, Bergstad and Godø 2003, Sutton et al. 2008). To date, few ecological studies have focused on the ridge, and hence, little is known about the fauna and ecology of MAR communities.

In 2001, the Census of Marine Life, a 10-year international effort to assess the diversity, distribution, and abundance of marine life, enacted a field project titled *Patterns and Processes of the Ecosystem of the Northern Mid-Atlantic* (MAR-ECO). This project aimed to describe and understand the patterns of distribution, abundance, and

trophic relationships of organisms inhabiting and associated with the northern MAR between Iceland and the Azores (Bergstad 2002). Describing the ecological processes that cause variability in these patterns is fundamental to understanding the influence of the MAR on this dynamic ecosystem.

One goal of MAR-ECO was to determine if the trophic structure of the northern MAR ecosystem is similar to that of continental slope regions of the eastern and western Atlantic. The presence of the MAR in the bathypelagic realm, and to a lesser extent in the mesopelagic realm, provides the potential for unique faunal interactions and nutrient availability. Elevated levels of primary productivity and chlorophyll, which are often associated with seamounts, mid-ocean ridges, and frontal zones in oligotrophic regions (Genin and Boehlert 1985, Dower et al. 1992, Muriño et al. 2001), have the potential to support enhanced secondary production and higher order epi- and mesopelagic biomass. Benthopelagic organisms associated with the ridge surface are supported through resuspension of sediment and through predation on pelagic fauna. Non-migrating pelagic fauna become susceptible to predation through advection to the ridge by water currents, while vertically migrating mesopelagic fauna become trapped by the elevated seafloor during their daily migratory descent (Genin and Dower 2007, Porteiro and Sutton 2007). Due to the potential for enhanced nutrient availability and faunal interactions at the MAR, this ecosystem may support a unique community and trophic structure compared to off-ridge waters.

Pelagic fish community structure of the Mid-Atlantic Ridge

To investigate the diversity, community structure, and trophic ecology of organisms inhabiting the MAR, MAR-ECO sampled the epi-, meso-, and bathypelagic fauna during a two-part expedition to the ridge during June-July, 2004 aboard the Norwegian vessel R/V *G.O. Sars*. These cruises were two of many MAR-ECO sampling expeditions to the MAR with the goal of assessing the occurrence, distribution, and ecology of animals and animal communities along the ridge between Iceland and the Azores (Figure 1). Leg 1 of this expedition sampled the pelagic fauna and is the focus of my thesis.

Sampling during leg 1 resulted in the collection of 205 fish species and the classification of the faunal composition within four sections along the MAR and five depth zones (see Methods for description of depth zones). A detailed description of the community structure of the MAR is provided by Sutton et al. (2008). The MAR ecosystem is unique in many ways compared to the surrounding areas of the eastern and western Atlantic. A decrease in faunal abundance and biomass with increasing depth is typically expected for open ocean ecosystems; however, the pelagic MAR fauna exhibited higher than expected abundance and biomass at bathypelagic depths (Sutton et al. 2008). Depth distributions of some MAR fishes were unique in that many species were found over the ridge at depths deeper and shallower than previously recorded, and demersal fish biomass was highest at stations near the summit of the ridge (Bergstad et al. 2008). Community composition of mesopelagic fishes along the ridge was fairly consistent north of the Sub-polar Front, a prominent hydrologic feature crossing the

MAR between 45-52°N, which appeared to act as a boundary to the northward distribution of many southern species.

Fishes of the families Myctophidae, Gonostomatidae, Microstomatidae, Stomiidae, and Melamphidae were abundant throughout the ridge with vertically migrating myctophids dominating the 200-750 m depth zone. Forty-five myctophid species were caught along the ridge, however only nine species comprised more than 1% of the total myctophid abundance by number. In accordance with typical trends of abundance and species richness at high latitudes, the fish assemblage in the three northern ridge sections in the 200-750 m depth zone comprised only a few abundant species, predominantly myctophids. There was a shift in community composition at the Azorean Zone (AZ) ridge section within the same depth zone. Here, species richness was much higher than farther north and the abundance of each species decreased.

The most abundant fish collected from the ridge during leg 1 of the MAR-ECO cruise was the myctophid *Benthoosema glaciale*. This species made up over half of the abundance by number and one quarter of the biomass in the three northern ridge sections from 0-750 m but only 6% and 4%, respectively, in the AZ (Sutton et al. 2008).

Benthoosema glaciale was also very abundant in deeper waters up to 1500 m in the Faraday Seamount Zone (FSZ) and AZ due to cooler waters occurring deeper at lower latitudes. While *B. glaciale* exhibited a wide geographic distribution across all four ridge sections, other species, such as *Protomyctophum arcticum*, appeared to be more limited in their distribution. *Protomyctophum arcticum* was numerically abundant in the two northern ridge sections with only a few individuals caught at the FSZ and was not captured in the AZ. The distributions of several myctophid species were limited to a

single ridge section, notably the AZ. In this ridge section, 29 myctophid species made up half of the abundance in the 0-750 m depth zone and the myctophid *Lobianchia dofleini* replaced *B. glaciale* as the numerically dominant species, making up 19% of the abundance and 7% of the biomass (Sutton et al. 2008). The myctophid *Hygophum hygomii*, was unique in that it was a moderately abundant species (2.7% by number) found only at the AZ.

Much is known of the feeding ecology of *B. glaciale* in the North Atlantic; however, active carbon transport by myctophids in this area has not been studied. Very little information exists on the feeding ecology of other species, such as *P. arcticum* and *H. hygomii*, despite their high abundance. Notwithstanding the ample diet data for some North Atlantic myctophids, comprehensive feeding ecology of myctophids inhabiting the MAR, the largest topographic feature in the Atlantic Ocean, is unknown. Being that myctophids were the most abundant fishes collected from the MAR, and the importance of these fishes as consumers of plankton and prey for many higher order predators, information on the feeding ecology of and carbon transport by these fishes is necessary for an accurate portrayal of food web structure and carbon cycling in the MAR ecosystem.

Objectives and significance of the study

The main objective of this study was to describe and quantify the feeding ecology of MAR myctophids. A secondary objective was to quantify the contribution of vertically migrating myctophids through the active transport of carbon to the MAR biological pump. The feeding ecology and trophic importance of many species of myctophids from

around the world have been studied; however, neither the diets of myctophids inhabiting the ecologically distinctive MAR ecosystem nor the potential for carbon transport by vertically migrating MAR myctophids have been investigated. To accomplish the first objective, the diets of three myctophid species— *B. glaciale*, *P. arcticum*, and *H. hygomi* were investigated by quantifying the prey composition using weight, abundance, and frequency of occurrence indices. To relate the dietary information to the energy requirements and changes in diet with growth of each species, daily consumption was calculated and ontogenetic dietary shifts were explored. Multivariate analyses were used to determine how fish size and different environmental variables influence variance in the diet. To accomplish the second objective, the amount of carbon transported via respiration, excretion, and egestion to mesopelagic depths by vertically migrating MAR myctophids was quantified. This allowed for an estimation of the extent to which MAR myctophids contribute to active carbon transport in comparison to passive sinking of POC, and provide the first estimate of myctophid active transport in the North Atlantic Ocean.

The results from this study provide a comprehensive account of the diet of three abundant mesopelagic species of myctophids from the northern Mid-Atlantic Ridge during the months of June and July. This time of year in the North Atlantic represents an active feeding period for mesopelagic fishes, corresponding with spring phytoplankton blooms and subsequent zooplankton blooms. As a result of the high relative abundance and biomass of myctophids at the MAR, they have the potential to impart heavy predation pressure on zooplankton and to provide an important source of carbon export out of the euphotic zone through metabolism of surface-consumed food at midwater

depths. Estimates of active transport by mesopelagic fishes are limited, and do not exist for the MAR. These data provide carbon transport estimates for the most abundant vertically migrating, mesopelagic fish family along the MAR that can be used in biogeochemical models that simulate and predict total carbon flux from the euphotic zone. Additionally, due to their intermediate trophic position, information on the diet and feeding ecology of myctophids from the ridge is essential to the successful construction of a MAR ecosystem food web to achieve an understanding of the trophodynamics of the geographically and hydrodynamically unique MAR ecosystem.

METHODS

Sampling procedure

Myctophids were collected during the R/V *G.O. Sars* research expedition to the Mid-Atlantic Ridge (Iceland to the Azores) during June-July, 2004. Two double-warp, multi-cod end midwater trawls were used to sample the ridge fauna at discrete depth zones. The macrozooplankton trawl has a 6 x 6 m² mouth opening, 6 mm stretched mesh throughout its length, and was equipped with five opening and closing cod ends. The Åkra trawl has a 20-35 m vertical mouth opening, 110 m door-spread, graded mesh to 22 mm (stretched), and was equipped with three multiple opening and closing cod ends.

Predefined stations along the ridge were sampled discretely within five depth categories: 0-200, 200-750, 750-1500, 1500-2300, and >2300 m in four ridge sections (Figure 1). Average tow duration was 3:43 (hours: minutes) (maximum 6:52, minimum 0:59). Each net was open for an average of 0:53 (maximum 4:46, minimum 0:08). Samples were classified as day (D), dusk (DN), night (N), or dawn (ND) with dusk and dawn samples defined as the start time of the net being one hour before to one hour after sunset and sunrise, respectively (Sutton et al. 2008). Once on board, specimens were sorted and either frozen, or preserved in 10% buffered formalin. Preserved samples were identified and transferred to 70% ethanol in the laboratory. For additional detail concerning net sampling aboard the R/V *G.O. Sars* see Wenneck et al. (2008).

Myctophid selection, dissection, and prey identification

The three species included in this study, *Benthoosema glaciale*, *Protomyctophum arcticum*, and *Hygophum hygomii* were chosen because they fulfilled multiple criteria

that were needed to obtain a representative sample of the myctophid assemblage in order to investigate trophic ecology and carbon transport. Each species was abundant, occurred primarily in the mesopelagic zone, and was known to conduct diel vertical migration. *Benthosema glaciale* was very abundant at all of the four ridge sections and was captured in many tows at different depths and times throughout the day. *Protomyctophum arcticum* was caught in high numbers at the two northern ridge sections at several different depth and time-of-day combinations. *Hygophum hygomii* was caught only at the southern ridge section, and while the limited geographic distribution restricted the number of possible combinations of depth and time of capture, their numbers still allowed for an adequate description of the diet. The unique geographic distribution of each species allowed for comparisons not only among species, but also across ridge sections and varying environmental regimes.

A subset of specimens from the total catch of the three species was randomly selected for measurement and dissection from as many geographic-location, depth, and time-of-day combinations as were available. A total of 380 fish belonging to three species was included in this study: 265 *B. glaciale*, 76 *P. arcticum*, and 39 *H. hygomii*. The standard length of each fish was measured to the nearest 0.1 mm from the tip of the snout to the posterior edge of the caudal peduncle. The stomach and intestines were removed and contents were identified to the lowest possible taxonomic level using a Nikon SMZ 1000 dissecting microscope. Diet descriptions and analyses include prey from stomachs only. Intestinal prey were not included in the diet description due to the tendency for advanced digestion and low taxonomic resolution. Prey types that were observed infrequently were grouped with more common genus or family classifications

to avoid small sample sizes. Diet indices were calculated for the lowest taxonomic level of grouped prey types that provided adequate sample size (Table 1) as well as broad prey categories at the subclass level (e.g., copepod).

Prey measurements

The length and width of each prey item was determined to the nearest 0.01 mm using Image Pro Plus 5.0 software. Cephalosome and urosome length and width measurements were determined for copepods. Since hooks were often all that remained of chaetognaths in the guts, a maximum hook length to body length regression for Pacific *Sagitta elegans* (Terazaki 1993) was used to estimate body length, and a head width to body length ratio for the same species (Pearre 1980) was used to estimate body width. Total length and width were determined for all remaining prey for which body measurements were possible. For well-digested prey, average body measurements from intact, related taxa were used. Body measurements of prey items were used to calculate body volume using formulae for the most similar geometric shape. Prey volume was then used to determine wet weight (assuming specific gravity = 1.0 g cc⁻¹). Crustacean dry weight was calculated as 20% of wet weight and carbon as 40% of dry weight (Silver and Gowing 1991, Steinberg et al. 1998). Conversion factors for other, less abundant prey taxa were utilized as described in Larson (1986) and Steinberg et al. (1998).

General diet description

The diet of each myctophid species was summarized using three diet indices, percent frequency of occurrence, percent composition by number, and percent dry weight

after Hyslop (1980). The indices, represented below as $\%I_j$, were calculated using a cluster sampling estimator (Buckel et al. 1999, Latour et al. 2008) of the form:

$$\%I_j = \frac{\sum_{i=1}^n M_{ik} q_{ik}}{\sum_{i=1}^n M_{ik}} \times 100 \quad (1)$$

such that

$$q_{ik} = \frac{\sum_{k=1}^{n_k} w_{ijk}}{\sum_{j=1}^{n_j} \sum_{k=1}^{n_k} w_{ijk}} \quad (2)$$

where n is the number of cod ends containing predator k , M_{ik} is the number of predator k collected in cod end i , n_j is the number of prey types observed in stomachs of all predator k , and n_k is the number of predator k stomachs examined. In equation (2), q_{ik} represents the proportion of occurrence, abundance, or weight of each prey type in each cod end.

Diet composition indices were calculated as a weighted average of q_{ik} with the abundance of each predator, M_{ik} , as the weighting factor. The variance for each diet index was calculated as

$$\text{var}(\%I_j) = \frac{1}{n\bar{M}^2} \frac{\sum_{i=1}^n M_{ik}^2 (q_{ik} - I_j)^2}{n-1} \times 100^2 \quad (3)$$

after Latour et al. (2008), where \bar{M} is the average number of predator k collected in a cod end.

Ontogenetic and spatial changes in diet

The diets of many fishes change as they increase in size due to an increase in gape allowing them to exploit bigger or different prey. To examine the effect of fish size on the diet, individuals of each species were grouped into narrow size classes with the members of each class having a relatively similar diet composition. *Benthoosema glaciale* and *P. arcticum* were grouped into 5 mm size classes and the proportion of dry weight of each prey type was calculated for each size class. The narrow size classes were grouped into broader categories with similar prey composition based on prey weight using cluster analysis (Euclidean distance, average linkage method) and a scree plot was used to determine the number of clusters.

Canonical correspondence analysis (CCA, ter Braak 1986) is a method which extracts the major gradients in the data that can be accounted for by the measured explanatory variables (McGarigal et al. 2000). For *B. glaciale* and *P. arcticum*, CCA was used to investigate the relationship between diet, ridge section (RR, CGFZ, FSZ, AZ; see Figure 1), depth zone (0-200, 200-750, 750-1500, 1500-2300, >2300 m), and time of day (day, dusk, night, and dawn). Each element of the response matrix for the CCA was the mean percent weight of a given prey type in a particular depth, ridge-section, and time-of-day combination. In CCA, variability is explained by the canonical axes. The canonical axes are linear combinations of the independent explanatory variables which are correlated to the dependent variables, in this case weighted averages of prey. Significance of the explanatory variables was determined using ANOVA, and a biplot was constructed to explore the relationships between the explanatory variables and prey weight. The CCA was performed using R version 2.12.0.

Gastric evacuation and daily consumption

Daily consumption was calculated using an evacuation rate model based on Elliott and Persson (1978). Consumption (C_d) was calculated as

$$C_d = 24h \cdot E \cdot \bar{S}_{kr} \quad (4)$$

where 24 is the number of hours in a day, E is the evacuation rate, and \bar{S}_{kr} is the average stomach content weight of predator k from ridge section r . Evacuation rates at ridge-section specific temperatures were determined using a regression of compiled myctophid gut evacuation rates and temperatures ($E = 0.0942e^{0.0708t}$, where t represents temperature) from Pakhomov et al. (1996). Due to the wide latitudinal distribution of the sampling area, myctophids experienced different temperatures at their daytime depths (200-750 m, depth zone 2) between ridge sections. Depth zone 2 is the depth at which myctophids in this study are assumed to reside during the bulk of digestion. Consumption was calculated separately for each ridge section due to evacuation rate dependence on temperature.

Active carbon export by diel vertical migration

Active carbon export to below 200 m via respiration of CO₂, excretion of dissolved organic carbon (DOC), and egestion of particulate organic carbon (POC) in the form of fecal pellets was determined only for the RR and AZ. Migrator biomass, defined as the difference between night and day integrated myctophid biomass in the 0-200 m depth interval, could not be determined at the CGFZ and FSZ due to the lack of sufficient diel sampling at these ridge sections. CO₂ flux was calculated using the following equation from Dam et al. (1995)

$$F = B \cdot R \cdot 12h \quad (5)$$

where F is the CO₂ flux by migrant myctophids (mg C m⁻² d⁻¹), B is the biomass of migrant myctophids integrated to 200 m (mg DW m⁻²), R is the weight-specific respiration rate at temperatures experienced by myctophids at their day time residence depths at the RR or AZ (6.6 or 11.8°C, respectively; calculated using a myctophid oxygen consumption versus temperature regression reported in Donnelly and Torres (1988), which was converted to CO₂ respired using carbon and oxygen atomic ratios), and $12h$ is the assumed length of time myctophids spend at depth over a 24-h day. A respiratory quotient of 0.8 was used in the calculation of R (Brett and Groves 1979). DOC excretion information for fishes is lacking, so the relationship of CO₂ respiration to DOC excretion in zooplankton (DOC excretion = 31% • CO₂ respiration) reported by Steinberg et al. (2000) was used to estimate DOC excretion in myctophids. POC egestion at depth was calculated using the prey carbon conversions discussed above. It was assumed that 100% of stomach and intestinal contents of fish caught at the surface would be released below 200 m. The average amount of carbon per unit dry weight of fish biomass was determined for *B. glaciale* and *P. arcticum* and multiplied by the integrated migrator biomass at the RR or AZ and by 12 hours. Myctophid dry weight was determined using a wet weight-standard length regression for each species (Fock and Ehrich 2010) and a wet weight-dry weight ratio (DW/WW = 22.64%) based on an average of compiled wet weight-dry weight ratios for many individual myctophid species (Carmo pers. comm.).

RESULTS

General diet description

Benthosema glaciale

Fifty-nine different prey types were identified in 201 positive stomachs (75% of all stomachs dissected) to an array of taxonomic levels depending on the extent of digestion. Copepods constituted the bulk of the diet by weight (52%), were the most frequently occurring prey category (93% of stomachs), and were the most abundant prey (90% of all prey items by number). The copepod *Calanus finmarchicus* was the predominant copepod in the diet of *B. glaciale* and made up over one quarter of the diet by weight alone. Euphausiids were another major component of the diet, constituting 37% of the diet by weight and occurring in 21% of stomachs, but were consumed in low abundance (2% of all prey items by number). Chaetognaths and ostracods constituted 6% and 3% of the diet by weight, respectively, while the remaining prey categories—amphipods, gelatinous prey, fishes, polychaetes, pteropods, digested crustaceans, and unidentified prey, made up 1% or less of the diet by weight.

Protomyctophum arcticum

The diet of *P. arcticum* comprised 26 different prey types from 74 positive stomachs (97% of all stomachs dissected) and was made up primarily of copepods (68%) and euphausiids (25%) by weight. Nearly all *P. arcticum* stomachs contained copepods (93% of stomachs) with the large copepod *Paraeuchaeta norvegica* making up the highest proportion of copepod weight (15%). Ostracods occurred in 37% of stomachs but constituted only 6% of the diet by weight and 12% by number. Digested crustaceans and

unidentified prey were the only other prey found in the diet of *P. arcticum* and made up less than 1% of the diet by weight and number.

Hygophum hygomii

Eighteen different prey types from 28 positive stomachs (72% of all stomachs dissected) were identified in the diet of *H. hygomii*. Euphausiids made up the highest proportion of the diet by weight (53%) and occurred in 57% of stomachs; however, they accounted for only 7% of all prey items by number. Ostracods were eaten frequently and in high numbers, occurring in 80% of stomachs, making up 37% of the diet numerically, and constituting one quarter of the diet by weight. Copepods, mainly *Pleuromamma sp.*, *Candacia sp.*, and euchaetid species, were the most frequently consumed prey category (84% of stomachs), and made up half of the diet by number and 15% by weight. Fishes, amphipods, pteropods, and unidentified prey each made up 5% or less by weight, although amphipods were found in over half of stomachs.

Ontogenetic and spatial changes in diet

Benthoosema glaciale

The size range of *B. glaciale* included in this study was 10.7-66.9 mm standard length (Figure 2). Cluster analysis and a scree plot indicated three clusters of *B. glaciale* based on diet composition and fish size separated into 5 mm size classes (Figures 3A and B). The clusters of size classes did not parse out into discrete groups of sequential fish sizes (i.e. small, medium, large). Instead, medium and large size classes (>20 mm) were intermixed within two clusters while the smallest sizes (10-19.9 mm) clustered together.

The clusters closely reflect the proportion of euphausiid weight in the diet. Fish in cluster A (Figure 3A) did not contain euphausiids, fish in cluster B possessed a high proportion of euphausiid weight in the diet, and fish in cluster C contained a low proportion of euphausiid weight in the diet. Due to the lack of evidence of an ontogenetic shift in the diet of *B. glaciale* beyond the smallest size classes, fish size was not included in subsequent analyses.

Canonical correspondence analysis (CCA) indicated *B. glaciale* dietary changes in relation to ridge section ($p = 0.005$) and time of day ($p = 0.025$) were significant at $\alpha = 0.05$ whereas depth ($p = 0.25$) was not significant (Figure 4). The three explanatory variables included in the CCA, depth, ridge section, and time of day, accounted for 30% of the variability in the diet, collectively. The first and second canonical axes accounted for 34% and 29% of the explainable variation, respectively. Ridge section corresponded more closely with the first canonical axis than the second, and accounted for a greater proportion of the explainable variation. The remaining significant explanatory variable, time of day, was more closely correlated to the second axis.

Prey items constituting the bulk of the diet of *B. glaciale* from the three northern ridge sections were similar to each other but different from prey items in the diet of *B. glaciale* from the AZ (Figure 5A). The diets of *B. glaciale* from the RR, CGFZ, and FSZ were comprised mainly of euphausiids, 35%, 44%, and 65% by weight, respectively. The copepod *Calanus finmarchicus* ranked second in the RR and CGFZ, constituting 31% and 25% of the diet by weight, respectively, while *P. norvegica* made up 6% of the diet by weight in the RR and 7% in the CGFZ. After euphausiids, ostracods and *P. norvegica* constituted 11% and 6% of the diet by weight, respectively, in the FSZ. The diets of *B.*

glaciale from the AZ differed from those of the three northern ridge sections in that ostracods made up 59% of the diet by weight. *Pleuromamma* copepods (7% by weight) were the only other prey to make up greater than 5% of the diet by weight in *B. glaciale* from the AZ. Polychaetes were only found in diets of myctophids from the RR, and fish prey and pteropods were only identified in diets from the FSZ. Gelatinous prey was found in the stomachs of fish from the RR, FSZ, and AZ.

The diet of *B. glaciale* collected during the day was comprised mainly of *C. finmarchicus* and euphausiids, 31% and 29% by weight, respectively (Figure 5B). Unidentified Calanidae copepods were the primary prey (42% by weight) in the night time diets, while chaetognaths (67%) were the predominant prey at dawn. *Calanus finmarchicus*, pteropods, and fish prey were only identified in fishes collected during the day and polychaetes were only found in dawn samples. It is unlikely that *B. glaciale* did not consume *C. finmarchicus* during the night, rather that poor taxonomic resolution prohibited identification to genus or species level.

Protomyctophum arcticum

The size distribution of *P. arcticum* was 18-44.5 mm standard length (Figure 2). The cluster analysis and scree plot (data not shown) indicated there was no ontogenetic change in the diet and, therefore, fish length was not included in the CCA. CCA indicated depth ($p = 0.03$) to be the only significant factor at $\alpha = 0.05$ whereas ridge section ($p = 0.46$) and time of day ($p = 0.23$) were not significant. The three explanatory variables included in the CCA, depth, ridge section, and time of day, accounted for 38% of the variability in the diet, collectively (Figure 6). The first and second canonical axes

accounted for 38% and 32% of the explainable variation, respectively. Depth zone corresponded more closely with the second canonical axis.

The main difference in *P. arcticum* diet with respect to depth was the high proportion of euphausiids (31%) in fish collected from depth zone 2 (200-750 m) and the absence of euphausiids in fish from depth zone 1 (0-200 m; Figure 7). *Paraeuchaeta norvegica* was identified in greater proportion in depth zone 2 (18%) than depth zone 1 (7%). The main components in the diets of fish from depth zone 1 were the copepod *Metridia sp.* (17%), ostracods (16%), *C. finmarchicus* (13%), and copepods of the family Aetideidae (12%).

Hygophum hygomii

The size distribution of *H. hygomii* was 27.7-56 mm standard length. There were too few *H. hygomii* at the smallest and largest sizes to allow for cluster analysis of this species. Additionally, since *H. hygomii* was only caught at the AZ and only during the day, CCA was not performed for this species.

Species interaction and the effect on spatial changes in diet

To investigate the effect of co-occurrence of *B. glaciale* and *P. arcticum* on the feeding ecology of these two species, CCA was performed for two scenarios in which fish species was added as an explanatory variable. In one scenario only cod ends in which both *B. glaciale* and *P. arcticum* were caught were included, and in another scenario all cod ends that caught at least one of the two species were included. When all cod ends that caught at least one of the two species were included in the CCA (Figure

8A), ridge section and fish species were significant ($p = 0.005$ and $p = 0.01$, respectively) at $\alpha = 0.05$, while depth zone and time of day were not ($p = 0.79$ and $p = 0.12$, respectively). The four explanatory variables included in the CCA, depth, ridge section, time of day, and fish species, accounted for 25% of the variability in the diet, collectively. The first canonical axis accounted for 28% of the explainable variation while the second axis accounted for 23%. Ridge section corresponded more closely with the first canonical axis and accounted for a greater proportion of the explainable variation, while fish species corresponded more closely to the second axis. Due to the difference in distribution of these two species, it was not surprising that ridge section and fish species were significant.

When only cod ends that contained both species were included in the CCA (Figure 8B), fish species was significant ($p = 0.05$) at $\alpha = 0.05$ and time of day approached significance ($p = 0.08$) which indicated that these two species, when caught together, had significantly different diet compositions, and diets of both species differed slightly between day, night, and dawn. The four explanatory variables accounted for 34% of the variability in the diet with the first canonical axis accounting for 33% of the explainable variation and the second axis accounting for 24%. Fish species corresponded more closely to the first canonical axis and time of day corresponded more closely with the second axis.

Gastric evacuation and daily consumption

Gastric evacuation rates were calculated for each myctophid species using average water temperatures experienced in the 200-750 m depth zone in each ridge

section. From the northernmost ridge section to the southernmost, average water temperatures were 6.6 °C (RR), 4.9 °C (CGFZ), 7.6 °C (FSZ), and 11.8 °C (AZ), with the decline in temperature at the CGFZ due to the unique physical characteristics of the Subpolar Front, present in this area (Søiland et al. 2008). Evacuation rates increased with increasing temperature and ranged from 0.13-0.22 h⁻¹ (Table 2). The average total weight of prey in the stomachs of *B. glaciale* was highest at the RR (3.6 µg DW prey fish⁻¹) and for *P. arcticum* at the CGFZ (0.09 µg DW prey fish⁻¹). Average total weight of prey was lowest for *B. glaciale* in the AZ (0.02 µg DW prey fish⁻¹) and for *P. arcticum* in the RR (0.03 µg DW prey fish⁻¹). *Hygophum hygomii* was only caught at the AZ and the average total weight of prey in the stomachs was 0.92 µg DW prey fish⁻¹. Daily consumption rates per fish were calculated for each species at each ridge section (Table 2), converted to consumption per unit of average myctophid biomass at each ridge section, and were multiplied by the biomass of all myctophid species combined integrated to 2300 m to provide a range of possible daily consumption estimates of MAR myctophids. Estimated daily consumption of prey inferred for all MAR myctophids ranged from 0.34-42.02 µg DW m⁻² d⁻¹ at the RR, 1.54-28.37 µg DW m⁻² d⁻¹ at the CGFZ, 6.83 µg DW m⁻² d⁻¹ at the FSZ, and 0.72-3.35 µg DW m⁻² d⁻¹ at the AZ. Daily consumption in proportion to myctophid body weight was always less than 1% for each species regardless of ridge section.

Active carbon export by diel vertical migration

Active transport of carbon by diel vertically migrating myctophids was calculated for ridge sections at which both day and night tows were performed in depth zone 1 (0-

200 m) and for which night time myctophid biomass was greater than day time myctophid biomass in depth zone 1. The RR and AZ were the only ridge sections that met these criteria. Respiration of CO₂ by the 0-200 m integrated migrant myctophid biomass was 0.01 mg C m⁻² d⁻¹ at the RR and 0.27 mg C m⁻² d⁻¹ at the AZ (Table 3). Myctophid excretion of DOC (calculated as 31% of myctophid respiration-see Methods) was 0.003 mg C m⁻² d⁻¹ at the RR and 0.08 mg C m⁻² d⁻¹ at the AZ. Egestion of POC was determined for *B. glaciale* at the RR and AZ and for *P. arcticum* at the RR. *Hygophum hygomii* was only collected during the day and therefore migrant biomass and carbon export could not be calculated for this species. Egestion rate of POC by *B. glaciale* multiplied by the 0-200 m integrated migrant myctophid biomass resulted in export of 1.61 x 10⁻⁶ mg C m⁻² d⁻¹ at the RR and 1.71 x 10⁻⁴ mg C m⁻² d⁻¹ at the AZ. Substituting egestion rate of POC by *P. arcticum* resulted in export of 7.08 x 10⁻⁶ mg C m⁻² d⁻¹ in the RR. Total carbon transport by the migrant myctophid biomass in the RR and AZ was estimated as 0.014 and 0.353 mg C m⁻² d⁻¹, respectively.

DISCUSSION

General diet description

Benthoosema glaciale, *P. arcticum*, and *H. hygomii* were primarily zooplanktivorous; however, the zooplankton composition and weight, frequency, and abundance of prey varied among species. The overall diet composition of myctophids from the ridge agrees with previous diet studies of these species (discussed below); however, direct comparison to other studies of prey proportion in diets is not possible due to the difference in sampling estimator used in this study (Equations 1 and 2). When calculating diet indices of fish caught in active sampling gears it is important to consider the sampling design used to collect the fish, as well as the species' ecological characteristics. Fish are known to aggregate in response to environmental gradients, resource availability, and social behavior (Pitcher and Parrish 1993, Pakhomov and Yamamura 2010); therefore, active sampling gear (such as the macrozooplankton and Åkra trawls used in this study) are likely to collect groups of fish that are found together in space and time based on a commonality, such as food availability. These groups are likely to consume similar types of prey and in similar quantities and, thus, their diets are likely to be more comparable to each other than to groups collected at different times or locations (Latour pers. comm.). Therefore, in order to characterize the predatory impacts of these fishes at the population level, these groups of fishes, rather than the individual, should be considered the independent sampling unit (Bogstad et al. 1995, Buckel et al. 1999).

The simple random sampling (SRS) estimator is the predominant method used to calculate diet indices of pelagic fishes (Hopkins and Gartner 1992, Moku et al. 2000) and

assumes that fishes are evenly distributed in the environment and have an equal probability of capture (Cochran 1977). As discussed above, this assumption is often not the case and, hence, the SRS estimator is not an appropriate method to use for calculating diet indices of fishes with aforementioned ecological characteristics. In addition to considering the ecology of the species, the appropriate sampling estimator can be determined mathematically using the intracluster correlation coefficient (ICC, ρ) which measures the relationship of the variance between groups of fish caught in different cod ends to the variance within a group of fish caught in a single cod end. The parameter ρ can be estimated for each prey type as

$$\hat{\rho} = \frac{\hat{s}_b^2}{\hat{s}_b^2 + \hat{s}_w^2} \quad (6)$$

where \hat{s}_b^2 is the estimate of variance between groups and \hat{s}_w^2 is the estimate of variance within groups (Steel et al. 1997). As \hat{s}_w^2 decreases towards 0 (signifying stomach contents within cod ends are increasingly similar) ρ approaches 1. The ICC for several of the most common prey types in the diet for each species ranged from 0.48-0.74 for *B. glaciale*, 0.42-0.73 for *P. arcticum*, 0.84-0.98 for *H. hygomii*, indicating the diets of each species within cod ends tend to be more similar than between cod ends. As a result, a cluster sampling estimator, which treats the groups of fish in each cod end as the independent sampling unit, was used to calculate dietary indices of these three species from the MAR.

Of the three myctophid species included in this study, more is known about the feeding ecology of *B. glaciale* than *P. arcticum* or *H. hygomii*. The diet of *B. glaciale* from the MAR observed in this study was comprised predominantly of copepods by

weight, frequency of occurrence, and abundance. *Calanus finmarchicus* and euphausiids made up the bulk of the diet by weight, with many other copepod taxa, amphipods, ostracods, chaetognaths, pteropods, polychaets, fish, and unidentified gelatinous zooplankton being consumed as well. Although not commonly identified in the diet, myctophids do consume gelatinous prey. Several studies from the Gulf of Mexico reported some larval and adult myctophid species fed on gelatinous prey, with some larvae feeding almost exclusively on gelatinous zooplankton (Hopkins and Gartner 1992, Conley and Hopkins 2004). Hopkins and Gartner (1992) reported gelatinous prey in the diet of *Benthosema suborbitale*; however, to my knowledge, gelatinous prey has not been reported in the diet of *B. glaciale*. Gelatinous prey was identified in the stomachs of seven *B. glaciale* >40 mm from the MAR, equating to less than 1% of the numerical abundance of prey in the diet. Due to the rapid digestion of gelatinous material, this estimate represents an underestimate of gelatinous zooplankton in the diet of this species. The diet of *B. glaciale* from the MAR agreed well with many previous studies of this species which reported copepods, predominantly *C. finmarchicus*, *Pleuromamma spp.*, *Metridia spp.*, and *Paraeuchaeta norvegica*, to comprise the bulk of the diet while the fish also consumed euphausiids, ostracods, amphipods, pteropods, chaetognaths, and fishes (Gjøsæter 1973, Kinzer 1977, Kawaguchi and Mauchline 1982, Roe and Badcock 1984, Petursdottir et al. 2008).

The diet of *P. arcticum* from the MAR was comprised mainly of copepods, with *P. norvegica* constituting the bulk of the copepod component. Euphausiids and ostracods were the only other identifiable prey in the diet. In a study from the Rockall Trough in the North Atlantic, the diet of *P. arcticum* was also comprised mainly of copepods,

specifically *Pleuromamma spp.*, as well as other copepods, such as *Metridia sp.* and *Aetideus sp.*, ostracods, and amphipods (Kawaguchi and Mauchline 1982). In the Davis Strait west of Greenland, *C. finmarchicus* was the only identifiable prey of *P. arcticum* (Sameoto 1989). The diet of *H. hygomii* from the MAR, mainly euphausiids and copepods, also agreed well with previous studies; however, fish prey was surprisingly abundant, constituting 5% of the diet by abundance at the MAR. In previous studies at Great Meteor Seamount and in the Gulf of Mexico, *H. hygomii* fed on copepods, amphipods, chaetognaths, euphausiids, mysids, ostracods, pteropods and unidentified gelatinous prey (Hopkins and Gartner 1992, Pusch et al. 2004).

Diets of these three species likely reflect their different geographic distributions. *Benthosema glaciale* occurred at all four ridge sections but was considerably less abundant at the AZ, *P. arcticum* occurred at the three northern ridge sections, primarily the RR and CGFZ, and *H. hygomii* was collected only from the AZ. Sutton et al. (2008) identified a shift in the midwater fish assemblage composition from the three northern ridge sections to the AZ, and a similar pattern was also observed in the distribution of some copepod taxa. Gaard et al. (2008) found that the Sub-Polar Front (SPF) appeared to act as a boundary to the horizontal distribution of several copepod species. Most copepod genera that dominated north of the front were also present to the south but the species were often different. The front appeared to restrict the northward distribution of southern copepod genera more so than the reverse, as 14 genera were restricted to the south of the SPF whereas only 4 were restricted to the north (Gaard et al. 2008). Some of these patterns in copepod distribution were evident in the diet of the MAR myctophids in this study, and are discussed below.

Ontogenetic and spatial changes in diet

Once general diet characteristics are known, it is useful to investigate what impact certain biotic and abiotic variables have on the diet. Fish size is one factor that can influence the composition of the diet. As a fish grows, different prey sizes and taxa become available for exploitation and noting the changes in the diet is important in understanding the ontogenetic changes in the ecology of the species. To avoid bias associated with assigning fish to broad size bins with breaks at which dietary changes are expected to occur, and then comparing the diets among those specified size bins, *B. glaciale* and *P. arcticum* were, instead, assigned to small, 5 mm size bins, ensuring fish within those bins had a relatively similar diet, and cluster analysis was used to determine at what sizes dietary changes occurred. Again, due to a difference in methodology direct comparison of ontogenetic dietary changes cannot be made with other studies but general diet trends with size can be compared.

Cluster analysis indicated there were no ontogenetic changes in the diet of *B. glaciale* beyond the smallest size classes, although three clusters were resolved (Figures 3A and B). The formation of these clusters was driven mainly by the weight of euphausiids in the diet of fish within the 5 mm size classes. Cluster A contained the smallest *B. glaciale* size classes included in this study, 10-19.9 mm. These fish did not consume euphausiids but fed heavily on *Pleuromamma* copepods, ostracods, amphipods and unidentified calanoid copepods. Fish >20 mm consumed euphausiids and were clustered into two groups, those with a moderate proportion (cluster C) and those with a high proportion (cluster B) of euphausiids (by weight) in the diet. Kinzer (1977) found only *B. glaciale* >30 mm consumed euphausiids and amphipods, whereas diets of 20-24.9

mm *B. glaciale* in this study comprised 30% of the euphausiids by weight consumed by all size classes, and the smallest *B. glaciale* size class (10-14.9 mm) consumed the greatest proportion of amphipods. Size classes between 30-54.9 mm consumed the highest proportion of *C. finmarchicus* copepods, suggesting that as *B. glaciale* increases in size and larger prey items can be consumed, they do not exclude small prey items from the diet (Dalpadado and Gjørseter 1988, Sameoto 1988). Conversely, Kawaguchi and Mauchline (1982) found the largest *B. glaciale* (36.1-62.5 mm) to exclude the smallest copepods and substitute large prey such as euphausiids and fish. Similar trends of exclusion were identified in the diets of other myctophid species as well (Hopkins et al. 1996, Pakhomov et al. 1996).

Cluster analysis indicated there was no ontogenetic change in diet of *P. arcticum* sampled from the MAR, and only one cluster was identified. The main difference in the diet amongst the different size classes was the high proportion of euphausiids (77% by weight) in the largest size class 40-44.9 mm. Euphausiids were present in all other size classes except the smallest (20-24.9 mm) but in much smaller proportions. Larger *P. arcticum* also ate more of the large copepod *P. norvegica*. Ostracods were eaten in fairly even proportions across all size classes while smaller *P. arcticum* tended to feed more heavily on *Metridia* spp., *C. finmarchicus* and other calanoid copepods. To my knowledge, aside from larval *Protomyctophum thompsoni* (Sassa and Kawaguchi 2005), detailed data of *Protomyctophum* spp. diet by size was previously unknown.

Sufficient sample size to perform a cluster analysis was not available for *H. hygomii* but a general comparison of the diets within several size classes follows. The diet across the different size classes (25-29.9, 35-39.9, 40-44.9, 45-49.9, and 50-59.9

mm) was very similar with most prey types occurring in each size class. Each of the size classes consumed primarily euphausiids with the proportion of euphausiid weight ranging from 52-82% of all prey weight in the size class. All *H. hygomii* size classes also contained ostracods and the copepods *Pleuromamma spp.*, *Oncaea spp.*, and *Candacia spp.* Fish prey only occurred in the 45-49.9 mm size class and pteropods occurred only in the 40-44.9 mm size class. Pusch et al. (2004) reported the numerical diet composition of *H. hygomii* in 10 mm size classes from 20-70 mm standard length. Copepods were the most abundant prey in the diet of all size classes except the largest, of which amphipods were the most abundant. Ostracods, pteropods, and euphausiids were consumed in low numbers in all size classes. Data from this study agreed with Pusch et al. (2004) in that copepods were eaten in high numbers in each size class; however, ostracods were eaten in equal or greater amounts compared to copepods at small and large sizes and amphipods were eaten in low abundance.

In addition to fish size, spatial and temporal factors also influence diet composition. Several different water masses are present along the MAR within the study site (Søiland et al. 2008). Water masses have different sources and characteristics such as water temperature which can influence the distribution of zooplankton and fishes both latitudinally and vertically and which, in turn, influences the available prey. Most myctophids and zooplankton are diel vertical migrators to varying degrees, remaining in isolumines throughout the water column that minimize the risk of predation but maximize the opportunity for feeding (Pearre 2003, Cohen and Forward 2009, Ringelberg 2010, Staby and Aksnes 2011). Some plankton undergo extensive migrations of hundreds of meters, while others may only travel short distances (Angel 1989, Anderson and Sardou

1992). Depending on the depth and time of day at which myctophids feed, each species could be feeding on a different prey field which would result in unique dietary composition. Thus, time of day, depth, and latitude (represented by ridge section) were included in a CCA to investigate the influence of these explanatory variables on the variability in the diet.

The CCA indicated a significant change in the diet of *B. glaciale* with respect to ridge section and time of day. As previously mentioned, the zooplankton community composition south of the SPF differed from ridge sections north of the front for many species and the shift in *B. glaciale* diet in the AZ reflects this change (Figure 5A). The abundance of *C. finmarchicus*, the numerically dominant calanoid copepod north of the SPF, declined by two orders of magnitude to the south of the front. This decrease in *C. finmarchicus* abundance is reflected in the diet of *B. glaciale* as it was not identified in the diet south of the SPF. The dominant components of *B. glaciale* diet in the three northern ridge sections, *C. finmarchicus* and euphausiids, were replaced by ostracods in the AZ. The separation of the AZ and corresponding prey from the other ridge sections in the CCA biplot reflect these trends (Figure 4).

There were several interesting differences between the diets of *B. glaciale* caught during the day, night, and dawn (there was only one dusk sample and, thus, it was not included). The most surprising difference was the absence of *C. finmarchicus* from night and dawn samples while constituting 31% of the diet by weight of *B. glaciale* during the day. The absence of *C. finmarchicus* from the diet at night and dawn could be due to mismatch in vertical distribution of predator and prey; although, Gaard et al. (2008) reported *C. finmarchicus* was present from 0-2500 m at the MAR during the same

sampling period. Alternatively, the absence of *C. finmarchicus* could be an artifact of poor taxonomic resolution and conservative identification as unidentified Calanidae copepods made up 42% of night diets by weight. Chaetognaths made up a much greater proportion of the diet by weight of *B. glaciale* during dawn, constituting 67% of the diet by weight, versus 4% in day samples and <1% in night samples. However, the high proportion of chaetognath weight in dawn samples could be anomalous as there were only two (large) chaetognaths identified in these stomachs with the remaining prey consisting of small copepods and ostracods. Other differences in diet with regard to time of day include the presence of pteropods and fish only in day samples and polychaetes only in dawn samples, although these items made up a very small proportion of the weight and occurred in low abundance. The proportion of weight of most remaining prey items were fairly consistent in day and night samples, while less than half of prey types were identified in dawn samples.

Of the explanatory variables included in the *P. arcticum* CCA, the only significant variable was depth. *Protomyctophum arcticum* was collected primarily from depth zones 1 and 2 and these were the only depths included in the CCA. Vertical migration can influence the variety and quantity of prey available, however, vertical distribution and diel vertical migration data for adult *P. arcticum* are lacking, making it difficult to interpret how depth affects the diets of fish from different depths zones. Nafpaktitis (1977) and Hulley (1984) report depths of *P. arcticum* maximum abundance during the day and night in the North Atlantic to be 350 m (range of 250-850 m) and 250 m (range of 90-325 m), respectively, suggesting *P. arcticum* may exhibit a weak vertical migration. During the day, *P. arcticum* from the MAR exhibited typical patterns of abundance

corresponding to diel vertical migration, with abundance in depth zone 2 much higher than in depth zone 1; however, night time abundance was nearly equal in depth zones 1 and 2 which could be due to a sizeable proportion of *P. arcticum* abundance remaining at depth and not performing diel vertical migration (Watanabe et al. 1999). Alternatively, the limited night time sampling at the two northern ridge sections may not have been adequate to capture the true migratory pattern of this species, as the typical pattern of higher abundance at depth in the day, and surface waters at night, of *P. arcticum* was recorded during a subsequent MAR-ECO expedition to the CGFZ in 2009 (Cook et al. in press).

The main difference in *P. arcticum* diet between depth zones 1 and 2 was the presence of euphausiids only in stomachs collected during the day in depth zone 2, constituting 31% by weight of the diets from this depth. The observed difference in euphausiids with depth may be due to euphausiid diel vertical migration. However, abundances of euphausiids were much higher in depth zone 2 than in depth zone 1 during both day and night (unpublished data). It is unlikely that fish size is the underlying factor dictating euphausiid consumption as there was only a 4 mm increase in average *P. arcticum* size from depth zone 1 (28.4 mm SL) to depth zone 2 (32.1 mm SL) and the size range of *P. arcticum* that consumed euphausiids encompassed the average length of fish in each depth zone (28-44.5 mm SL). Other characteristics of *P. arcticum* diet from depth zones 1 and 2 include aetideid copepods, *C. finmarchicus*, *Metridia sp.*, and ostracods, all of which are known vertical migrators (Al-Mutairi and Landry 2001, Irigoien et al. 2004), constituting a considerably greater proportion of the diet by weight

in depth zone 1, while *P. norvegica* made up a greater proportion in depth zone 2. Other prey were generally consumed in similar proportions at both depths.

In an attempt to determine if co-occurring species consume similar prey, CCA was performed including diet data of both *B. glaciale* and *P. arcticum*. Both species exhibited different horizontal distributions along the MAR and, consequently, were exposed to different prey fields, especially *B. glaciale* south of the SPF. To remove the influence of contrasting distributions, only *B. glaciale* and *P. arcticum* that were caught together in the same cod end were included. Fish species was a significant explanatory variable which indicates the diets of these two species, when caught together, are significantly different. In many cod ends where both species were caught, prey items identified in the stomachs of one species were typically absent or consumed in much lower proportion by the other species (Table 4). Time of day also approached significance when only co-occurring samples were included, driven mainly by rare prey and prey types that made up a high proportion of the weight which were eaten at only one time of day. Although niche overlap is not calculated here due to a lack of consensus as to which measure is most accurate and least biased (Smith and Zaret 1982), these differences in diet may suggest that some degree of resource partitioning could exist to reduce competition. It must be kept in mind, as always, that the differences in the diet could partially be due to poor taxonomic resolution.

Daily Consumption

The maximum daily consumption as a percentage of dry body weight for myctophids in this study was 0.01%, below minimum values from previous studies.

Although a variety of methods have been used and direct comparisons are not possible, the consensus is that myctophids generally consume <1-6% of dry body weight per day, with most estimates closer to 1% (see table 6.2 in Brodeur and Yamamura (2005) and sources therein). Average water temperature in depth zone 2 was lowest at the CGFZ and highest at the AZ and, thus, calculated evacuation rates followed the same pattern since evacuation rate is typically positively correlated with temperature to a maximum (Table 2) (Elliott and Persson 1978 and sources therein). Daily consumption by *B. glaciale* was highest at the RR and decreased to the AZ, while daily consumption by *P. arcticum* increased from the RR to the CGFZ. *Hygophum hygomii* was only collected in the AZ and consumed a moderate amount compared to *B. glaciale*. Daily consumption estimates for MAR myctophids presented here are likely to be an underestimate as a result of the sampling design employed on the *G.O. Sars* cruise. Shallow depth zones were sampled first and, thus, myctophids collected in depth zones 1 and 2 would continue digesting for many hours after capture while the deeper depths were sampled. This prolonged digestion would result in an underestimation of prey abundance in stomachs and, consequently, underestimation of prey weight as a percentage of fish body weight. Additionally, estimation of daily consumption of diel vertically migrating subarctic myctophid species, which assumes only surface feeding at night, can be underestimated due to active feeding during the day at depth. If day time feeding is not accounted for, it could lead to an underestimate of the true daily consumption (Brodeur and Yamamura 2005). Although day time feeding was observed in both *B. glaciale* and *P. arcticum*, the number of feeding periods over a 24 hour cycle could not be discerned from stomach fullness data.

In order to accurately estimate the amount of prey consumed by the MAR myctophid assemblage, an accurate estimate of myctophid biomass is required. Midwater trawls have been the predominant tool used to estimate fish biomass in the past but acoustic measurements are becoming increasingly more common and are shedding light on inaccuracies of midwater trawls. Kaartvedt et al. (2012) estimated the sampling efficiency of a large (~400 m² mouth area) Harstad trawl using acoustics to verify the catch of *B. glaciale*. They found *B. glaciale* was capable of avoiding the large trawl to such an extent that the sampling efficiency was 14%. A similarly low sampling efficiency was determined by Koslow et al. (1997) for a medium-sized IYGPT trawl (105 m² mouth area). In the present study, myctophid biomass was estimated using the small (36 m² mouth area) macrozooplankton trawl since the fixed mouth area of this trawl allowed for a more accurate calculation of volume of water filtered than the large (~660 m² mouth area) Åkra trawl. Heino et al. (2011) determined the Åkra trawl to be more efficient at catching fish than the macrozooplankton trawl with a relative catchability of 2.3. Because *B. glaciale* appears to be capable of avoiding even large midwater trawls, the sampling efficiency of the macrozooplankton trawl could potentially be even lower than 14% for large, stronger swimming myctophids, while the smaller mesh of the macrozooplankton trawl would retain small fish better than the Åkra trawl.

The daily consumption by the MAR myctophid biomass reported in Table 2 is based on the myctophid biomass collected with the macrozooplankton trawl. If the 14% efficiency estimation reported by Koslow et al. (1997) and Kaartvedt et al. (2012) is applied here, the daily consumption of the MAR integrated myctophid biomass feeding in the 0-200 m depth zone at night ranges from 0.1-18 ug DW m⁻² d⁻¹ in the RR, 14 ug DW

$\text{m}^{-2} \text{d}^{-1}$ in the FSZ, and $4\text{-}18 \text{ ug DW m}^{-2} \text{ d}^{-1}$ in the AZ (myctophids were not caught at night in depth zone 1 at the CGFZ). Zooplankton biomass was not estimated at the MAR, so integrated zooplankton biomass estimates were used from Gallienne et al. (2001) in the area of $47^{\circ}\text{N } 20^{\circ}\text{W}$ in the North Atlantic during July, 1996 for the RR (reported carbon values converted to dry weight using the conversion carbon = 40% DW), and 0-200 m integrated values from the Bermuda Atlantic Time-series Study (BATS) station in the Sargasso Sea during June and July, 2004 (<http://bats.bios.edu/>, Steinberg et al. 2012) for the AZ to estimate the portion of the zooplankton biomass removed daily. Gallienne et al. (2001) reported zooplankton biomass in the North Atlantic was $763.5 \text{ mg DW m}^{-2}$ (vertically integrated to 200 m), and average nighttime zooplankton biomass at the BATS station was 735 mg DW m^{-2} . Applying the *B. glaciale* consumption rate to the RR and the *H. hygomii* consumption rate to the AZ integrated migrant myctophid biomass adjusted for gear efficiency resulted in the removal of <1% of zooplankton biomass at each ridge section every night. Estimated removal rates at the MAR were lower than daily zooplankton removal rates by myctophids reported in previous studies: 1-4% of zooplankton standing stock in the upper 150 m in the western North Pacific (Watanabe et al. 2002), 2% in the upper 200 m in the Gulf of Mexico (Hopkins and Gartner 1992), and 5-20% in the upper 300 m in the Southern Ocean (Pakhomov et al. 1999).

Active carbon export by diel vertical migration

Diel vertically migrating zooplankton contribute to the vertical export of carbon from the euphotic zone through respiration, excretion, and egestion (Longhurst et al.

1990, Schnetzer and Steinberg 2002), which could be an important source of carbon for non-migrating mesopelagic zooplankton, and for bacteria, which are ultimately reliant on surface-derived production (Steinberg et al. 2008). Diel vertically migrating fishes also have the potential to contribute to the active transport of carbon; however, only one study has quantified the contribution of mesopelagic fishes to the active transport of carbon to meso- and bathypelagic depths (Hidaka et al. 2001). Myctophids are the most abundant vertically migrating mesopelagic fishes in many areas, including the MAR, thus it is important to include active carbon transport for these mesopelagic fishes as potential contributors to the biological pump.

These estimates of active carbon transport out of the euphotic zone can be compared to passive POC flux measured by sediment traps to explore the relative importance of active vs. passive transport as components of the biological pump (Steinberg et al. 2000, Hidaka et al. 2001). Passive POC flux data from the MAR is currently unavailable and, hence, direct comparison to myctophid carbon export cannot be made for the MAR. There are, however, numerous measurements of sediment trap POC flux in the North Atlantic, mainly during the time of the North Atlantic spring bloom. Using results from several studies in the North Atlantic during April and May (Bender et al. 1992, Buesseler et al. 1992, Ducklow et al. 1993, Harrison et al. 1993, Martin et al. 1993), a range of passive POC flux values measured with sediment traps were compiled to compare to active transport by vertically migrating MAR myctophids. Sampling during the *G.O. Sars* cruise was performed during a post bloom period (Gaard et al. 2008) and, therefore, POC sinking rates would be lower than those during the spring bloom. The present study estimated the active transport of carbon out of the surface 200

m, but the compiled POC flux data were measured at 150 m and 300 m, so comparisons are made with flux data at both depths.

The migrant myctophid biomass was 5.2 mg C m^{-2} (integrated to 200 m) in the RR and 40 mg C m^{-2} in the AZ, and active transport of CO_2 , DOC, and POC during summer by MAR myctophids was $\leq 1\%$ of passively sinking POC in the North Atlantic at 150 m and 300 m (Table 3). Another study investigating active carbon export by myctophids in the western equatorial North Pacific Ocean found myctophid biomass (uncorrected for net sampling efficiency) was $249\text{-}462 \text{ mg C m}^{-2}$ from 0-160 m, and active transport through respiration and egestion was $1.2\text{-}2.2 \text{ mg C m}^{-2} \text{ d}^{-1}$, equivalent to 2.0-3.7% of passively sinking POC (Hidaka et al. 2001, stations 15 and 16). Hidaka et al. (2001) adopted the 14% sampling efficiency estimated by Koslow et al. (1997) which dramatically increased their migrating myctophid biomass estimate ($1778\text{-}3303 \text{ mg C m}^{-2}$) and, subsequently, carbon export ($8.4\text{-}15.4 \text{ mg C m}^{-2} \text{ d}^{-1}$, 14.3-26.4% of passively sinking POC). If the same sampling efficiency is applied to MAR myctophid biomass, active transport increases to $0.1 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the RR and $2.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the AZ, equivalent to 0.1-1.0% of sinking POC at 150 m and 0.3-3.5% at 300 m. The very high migrant myctophid biomass in the Pacific is the reason for the considerably higher active carbon transport estimated there compared to the MAR. MAR myctophid active transport is also lower than the long-term (1994-2011) annual average zooplankton active transport in the subtropical North Atlantic measured at the BATS station. There, zooplankton transported $4.1 \text{ mg C m}^{-2} \text{ d}^{-1}$ via respiration, excretion, and egestion at depth, which was, on average, 15% of sinking POC flux (Steinberg et al. 2012).

Due to the rapid decline of sinking POC with increasing depth, the carbon transported by vertically migrating myctophids—of which some species migrate to 1000 m or more, becomes increasingly important at greater depths. As a rough comparison, Honjo and Manganini (1993) report passive POC flux at 1000 m in the North Atlantic during April of $4.1 \text{ mg C m}^{-2} \text{ d}^{-1}$. Using corrected MAR myctophid biomass, the myctophid carbon export measured in this study would be equivalent to 61% of sinking POC at 1000 m. A few factors would decrease the amount of carbon transported to this depth, however. A smaller proportion of the migrating myctophid biomass resides at 1000 m during the day, and greater migration distance means increased time for digestion to occur resulting in a smaller proportion of POC actively exported out of the euphotic zone being released at 1000 m. Nevertheless, the high proportion of carbon exported by myctophids in relation to POC flux at greater depths reaffirms the importance of myctophids in the biological pump and sequestration of carbon in the deep sea, and suggests that myctophid active transport should be considered in carbon cycling models.

CONCLUSION

Overall, the diet of the three species of myctophids from the MAR analyzed in the present study agreed well with previous investigations of these species in off-ridge areas of the North Atlantic Ocean. However, the most abundant myctophid, *B. glaciale*, possessed some unique dietary and ecological characteristics not observed in this species elsewhere, such as consumption of gelatinous prey, and consumption of euphausiids and amphipods earlier in the fish's life history (i.e., at smaller fish sizes), which may suggest that the distinctive MAR ecosystem supports a unique food-web structure. It must be kept in mind, however, that this study provides information for only a limited period of time during the year and the conclusions cannot be extrapolated beyond the summer. Additional sampling during different times of year is necessary to determine if the differences observed in this study are characteristic of annual patterns at the MAR. Despite the limited temporal scale of this study, the resulting myctophid feeding data represents a necessary first step for the construction of a MAR food web for comparing the trophic structure of the MAR to continental slope regions of the eastern and western Atlantic.

Hidaka et al. (2001) provided an estimate of active carbon transport by myctophids in the Pacific Ocean and the current study provides the first estimate for Atlantic myctophids. Carbon transport by myctophids at the MAR during summer was low compared to sinking POC flux measured in the upper mesopelagic zone during the spring bloom, but may potentially account for a much greater proportion of exported carbon at lower mesopelagic depths. Additional spatial and temporal sampling and information on sampling efficiency of an array of trawl types are needed to develop more

robust estimates of active carbon transport by myctophids and other migrating fishes. Despite the high abundance of myctophids throughout the world's oceans, the present study is only the second to quantify the active transport of carbon to mesopelagic depths by these vertically migrating fishes. The inclusion of migrating fishes will lead to a more comprehensive view of the biological pump, which has implications for fueling deep-sea food webs, the microbial loop, and for sequestration of atmospheric CO₂.

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Table 1. Prey composition from stomachs of *Benthoosema glaciale*, *Protomyctophum arcticum*, and *Hygophum hygomii* collected during a cruise to the Mid-Atlantic Ridge during June-July, 2004. n is the sample size, %W is the percent dry weight, %N is the percent composition by number, and %F is the percent frequency of occurrence of each prey taxa. (-) indicates prey was absent.

Table 1.

Prey	<i>B. glaciale</i>			<i>P. arcticum</i>			<i>H. hygomii</i>					
	n	%W	%N	%F	n	%W	%N	%F	n	%W	%N	%F
Copepoda												
Calanoida												
<i>Aetideus sp.</i>	1	0.36	0.70	9.46	4	0.66	1.38	2.99	-	-	-	-
<i>Aetideus armata</i>	-	-	-	-	9	0.45	1.97	7.75	-	-	-	-
<i>Aetideopsis sp.</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Chiridiella sp.</i>	-	-	-	-	1	0.29	0.43	1.71	-	-	-	-
<i>Euchirella sp.</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Gaetanus sp.</i>	1	0.01	0.01	0.34	2	1.33	0.61	2.51	-	-	-	-
<i>Pseudochirella sp.</i>	1	0.00	0.01	0.34	-	-	-	-	-	-	-	-
Aetideidae	71	1.28	2.84	24.19	22	3.13	4.84	16.45	6	0.26	1.80	18.60
<i>Calanus sp.</i>	164	9.00	16.32	44.43	47	5.88	7.81	22.63	-	-	-	-
<i>Calanus finmarchicus</i>	388	27.88	51.38	71.73	94	8.14	12.20	14.78	-	-	-	-
Calanidae	116	2.88	4.56	5.80	11	1.18	1.87	7.68	46	1.33	7.16	54.83
<i>Candacia sp.</i>	-	-	-	-	39	1.13	6.99	65.41	-	-	-	-
<i>Candacia armata</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
Candaciidae	5	0.04	0.06	0.07	-	-	-	-	-	-	-	-
<i>Euchaeta sp.</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Paraeuchaeta sp.</i>	1	0.01	0.00	0.01	-	-	-	-	1	0.09	0.12	2.06
<i>Paraeuchaeta norvegica</i>	37	5.99	1.87	20.64	17	14.75	3.88	17.72	6	0.87	0.70	8.22
<i>Paraeuchaeta tonsa</i>	1	0.00	0.00	0.02	-	-	-	-	1	0.09	0.12	2.06
Euchaetidae	22	0.37	0.87	11.59	12	3.20	3.30	6.84	-	-	-	-
<i>Heterorhabdus sp.</i>	10	0.04	0.13	0.67	3	0.24	0.53	1.62	-	-	-	-
<i>Heterorhabdus compactus</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Heterostylites longicornis</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Heterostylites sp.</i>	12	0.00	0.03	0.20	1	0.26	0.43	1.50	-	-	-	-

Table 1. continued

Prey	<i>B. glaciale</i>			<i>P. arcticum</i>			<i>H. hygomii</i>					
	n	%W	%N	%F	n	%W	%N	%F	n	%W	%N	%F
Heterorhabdidae	-	-	-	-	1	0.01	0.15	1.54	-	-	-	-
<i>Metridia sp.</i>	87	0.21	1.25	4.21	71	6.27	12.20	22.46	-	-	-	-
<i>Metridia curticauda</i>	1	0.00	0.01	0.13	-	-	-	-	-	-	-	-
<i>Metridia lucens</i>	1	0.00	0.00	0.03	46	4.79	7.84	6.45	-	-	-	-
<i>Pleuromamma sp.</i>	218	1.42	4.18	39.42	37	4.67	8.45	27.24	82	2.17	17.19	80.24
<i>Pleuromamma abdominalis</i>	5	0.01	0.02	0.15	1	0.11	0.19	1.02	11	0.19	1.28	8.22
<i>Pleuromamma borealis</i>	5	0.01	0.02	0.08	-	-	-	-	-	-	-	-
<i>Pleuromamma gracilis</i>	2	0.00	0.00	0.04	-	-	-	-	-	-	-	-
<i>Pleuromamma robusta</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Pleuromamma xiphias</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
Metridiidae	48	0.19	1.03	3.87	20	3.06	4.54	17.38	-	-	-	-
<i>Paracalanus sp.</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
Spinocalanidae	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
Other Calanoida	129	1.26	3.04	8.86	50	7.95	9.65	38.24	39	1.55	7.53	56.43
Cyclopoid												
<i>Oncaea sp.</i>	21	0.02	0.77	9.84	2	0.02	0.29	2.62	27	0.06	5.36	55.23
Poecilostomatoida	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Sapphirina sp.</i>	1	0.00	0.01	0.06	-	-	-	-	-	-	-	-
Other Copepoda	20	0.52	0.98	12.42	10	1.39	2.11	10.45	4	0.15	1.02	14.82
Amphipoda												
<i>Themisto sp.</i>	19	0.34	0.12	2.21	-	-	-	-	17	4.92	5.12	51.59
<i>Themisto compressa</i>	10	0.09	0.06	0.40	-	-	-	-	-	-	-	-
<i>Phronima sp.</i>	2	0.10	0.07	1.64	-	-	-	-	-	-	-	-
Hyperiididae	1	0.45	0.11	0.30	-	-	-	-	-	-	-	-
Hyperiididae	14	0.21	0.28	1.37	-	-	-	-	1	0.25	0.27	1.83

Table 1. continued

Prey	<i>B. glaciale</i>			<i>P. arcticum</i>			<i>H. hygomii</i>					
	n	%W	%N	%F	n	%W	%N	%F	n	%W	%N	%F
Euphausiacea	34	28.68	1.82	17.33	14	24.93	2.61	13.36	34	68.84	7.49	56.56
Euphausiidae	25	8.35	0.51	4.08	-	-	-	-	-	-	-	-
Myodocopoda	247	3.11	3.72	19.22	55	4.87	9.70	35.17	162	14.45	37.12	80.37
<i>Conchoecia</i> sp.	2	0.01	0.01	0.04	-	-	-	-	-	-	-	-
<i>Conchoecia magna</i>	2	0.01	0.01	0.04	-	-	-	-	-	-	-	-
<i>Conchoecetta acuminata</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
<i>Conchoecilla daphnoides</i>	1	0.00	0.00	0.02	-	-	-	-	-	-	-	-
Conchoecinae	6	0.01	0.01	0.10	13	1.52	2.30	4.26	-	-	-	-
Pteropoda	1	0.00	0.01	0.02	-	-	-	-	-	-	-	-
<i>Limacina</i> sp.	1	0.00	0.01	0.02	-	-	-	-	-	-	-	-
Cavoliniidae	-	-	-	-	-	-	-	-	2	0.00	0.23	2.06
Gelata	6	0.10	0.37	1.02	-	-	-	-	-	-	-	-
Thaliacean	1	0.01	0.11	0.30	-	-	-	-	-	-	-	-
Chaetognatha	13	6.08	1.05	5.48	-	-	-	-	-	-	-	-
Polychaeta	1	0.01	0.01	0.05	-	-	-	-	-	-	-	-
Osteichthyes	2	0.08	0.04	0.00	-	-	-	-	1	3.49	0.20	5.40
Crustacea	8	0.07	0.05	0.18	2	0.51	0.55	2.14	-	-	-	-
Unidentified prey	23	0.79	1.56	11.83	1	0.40	0.17	2.05	2	0.14	0.31	7.46

Table 2. Evacuation rates and average daily consumption ($\mu\text{g DW d}^{-1}$) per fish at each ridge section (RR, Reykjanes Ridge; CGFZ, Charlie-Gibbs Fracture Zone; FSZ, Faraday Seamount Zone; AZ, Azorean Zone) for *Benthoosema glaciale*, *Protomyctophum arcticum*, and *Hygophum hygomii*. Values in parentheses are potential daily consumption ($\mu\text{g DW m}^{-2} \text{d}^{-1}$) by the biomass of all myctophid species at each ridge section integrated 0-2300 m using the average consumption per unit fish biomass of each of the three species. (-) indicates species was not collected from ridge section.

Ridge Section	T°C	Evacuation Rate (h^{-1})	Daily Consumption		
			<i>B. glaciale</i>	<i>P. arcticum</i>	<i>H. hygomii</i>
RR	6.6	0.150	12.99 (42.02)	0.11 (0.34)	-
CGFZ	4.9	0.133	6.99 (28.37)	0.28 (1.54)	-
FSZ	7.6	0.161	1.74 (6.83)	-	-
AZ	11.8	0.217	0.10 (0.72)	-	4.79 (3.35)

Table 3. Active transport of carbon ($\text{mg C m}^{-2} \text{d}^{-1}$) by diel migrating myctophids from the Reykjanes Ridge (RR) and Azorean Zone (AZ). Active transport of CO_2 and dissolved organic carbon (DOC) is for the 0-200 m integrated biomass of all myctophid species combined. Active transport of particulate organic carbon (POC) is the average carbon content of prey from night time 0-200 m *Benthosema glaciale* diets multiplied by the 0-200 m integrated biomass of all myctophid species combined. Total myctophid carbon export across 0-200 m is compared to average POC flux in the North Atlantic Ocean from different locations and depths* during April and May.

Ridge Section	CO_2	DOC	POC	Total	% of Average POC Flux*	
					150 m	300 m
RR	0.011	0.003	1.61×10^{-6}	0.014	0.01-0.02	0.02-0.04
AZ	0.270	0.084	1.71×10^{-4}	0.353	0.14-0.41	0.49-0.95

* POC flux ranged from 86-259 $\text{mg C m}^{-2} \text{d}^{-1}$ at 150 m and 37-72 $\text{mg C m}^{-2} \text{d}^{-1}$ at 300 m (Bender et al. 1992, Buesseler et al. 1992, Ducklow et al. 1993, Harrison et al. 1993, Martin et al. 1993)

Table 4. Proportion of prey weight in each species (BG, *Benthoosema glaciale*; PA, *Protomyctophum arcticum*) in

each cod end where both species were caught simultaneously. Color scale represents range of values, with warmer colors denoting higher proportions within each cod end.

Ridge Section	Cod end	Species	Aetideidae	<i>Aetideus</i> sp.	Calanidae	<i>Calanus</i> sp.	<i>Calanus finmarchicus</i>	Euchaetidae	<i>Paraeuchaeta norvegica</i>	Metridiidae	<i>Metridia</i> sp.	<i>Metridia lucens</i>	<i>Pleuromamma</i> sp.	Heterohabididae	Other Calanoida	Other Copepoda	Amphipoda	Hyperidae	Euphausiacea	Euphausiidae	Mydocalpoda	Crustacea	Gelata	Chaetognatha	Unidentified prey
RR 1002	BG	0	0	0	0	0	0	0	0.139	0.037	0	0	0.012	0	0.040	0	0.246	0	0	0	0.099	0	0.031	0.390	0.005
	PA	0	0.037	0	0	0	0	0	0	0.325	0.360	0	0.089	0	0.189	0	0	0	0	0	0	0	0	0	0
RR 1023	BG	0	0	0	0	0	0	0	0	0	0	0	0	0	0.146	0	0	0	0	0	0	0.064	0	0	0
	PA	0.032	0.010	0	0	0	0	0.298	0.403	0	0	0.016	0.030	0	0.367	0	0	0	0	0	0	0	0	0	0
RR 1028	BG	0.014	0	0.287	0.072	0	0	0	0.259	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PA	0	0	0	0.030	0	0	0.081	0	0	0.013	0	0	0	0	0.008	0	0	0	0.840	0	0.004	0.024	0	0
RR 1029	BG	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PA	0	0	0	0.165	0.510	0	0	0.136	0	0.064	0	0.009	0	0.095	0.020	0	0	0	0	0	0	0	0	0
RR 1030	BG	0.054	0	0.129	0.226	0	0	0	0.232	0.020	0	0	0.062	0	0.033	0	0	0	0	0	0	0	0	0	0.243
	PA	0	0	0.028	0.154	0.380	0	0	0	0.055	0.239	0	0	0	0.128	0	0	0	0	0	0.017	0	0	0	0
RR 1032	BG	0.030	0	0	0.035	0	0	0	0	0	0.017	0	0	0	0.181	0	0	0	0	0	0	0	0	0	0.713
	PA	0	0	0.069	0	0	0	0	0.618	0.099	0	0	0.041	0	0.173	0	0	0	0	0	0	0	0	0	0.025
RR 1037	BG	0	0	0.053	0	0.009	0.011	0	0	0	0	0	0.017	0	0.027	0	0	0	0.876	0	0	0	0	0	0.007
	PA	0.008	0.003	0	0.131	0.065	0	0	0	0	0.060	*	0	0	0.013	0.025	0	0	0.688	0	0.007	0	0	0	0
CGFZ 1044	BG	0.006	0	0.011	0.044	0.290	0.009	0.154	0.002	0.019	0	0.002	0	0	0.026	0	0.020	0.217	0.112	0.072	0.012	0	0	0	0.003
	PA	0.101	0	0	0	0	0.023	0.188	0	0.003	0.006	0.003	0	0	0.009	0.012	0	0	0.645	0	0.010	0	0	0	0
CGFZ 1077	BG	0.007	0	0.006	0.046	0.106	0	0	0	0.002	0.004	0	0.002	0	0.003	0	0	0.072	0.147	0.605	0	0	0	0	0
	PA	0.045	0	0	0.015	0	0	0.109	0.026	0	0.453	0.007	0	0	0.091	0	0	0	0.192	0	0.024	0	0	0	0.039
CGFZ 1078	BG	0	0	0.054	0.009	0	0	0	0	0.010	0	0	0.006	0	0.028	0	0	0	0.894	0	0	0	0	0	0
	PA	0.157	0	0	0.077	0	0	0.190	0	0.251	0	0.013	0.029	0.058	0	0	0	0	0	0	0.226	0	0	0	0

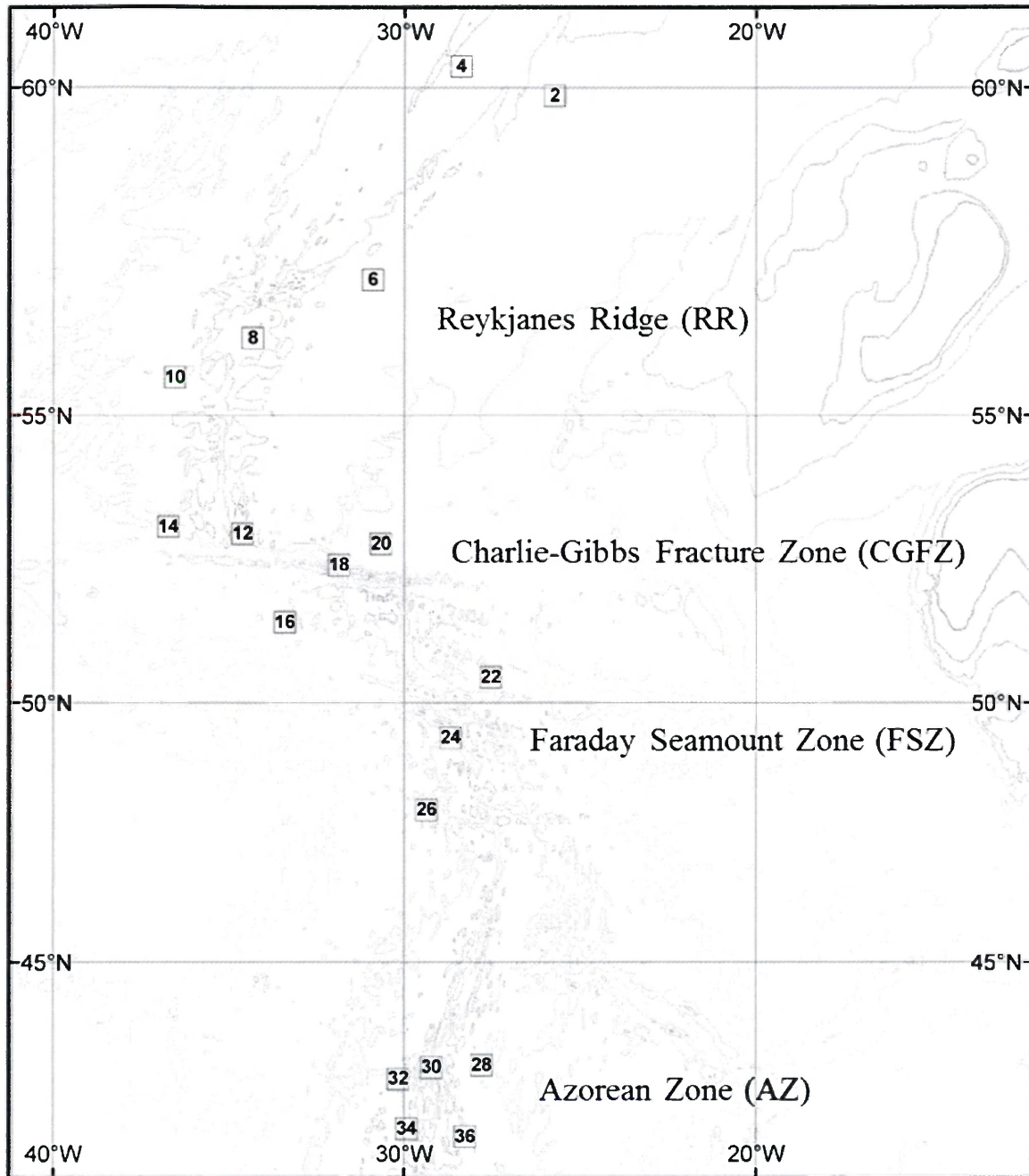


Figure 1. Trawl sampling stations at four ridge sections along the northern Mid-Atlantic Ridge from Iceland to the Azores during the 2004 R/V *G.O. Sars* MAR-ECO expedition.

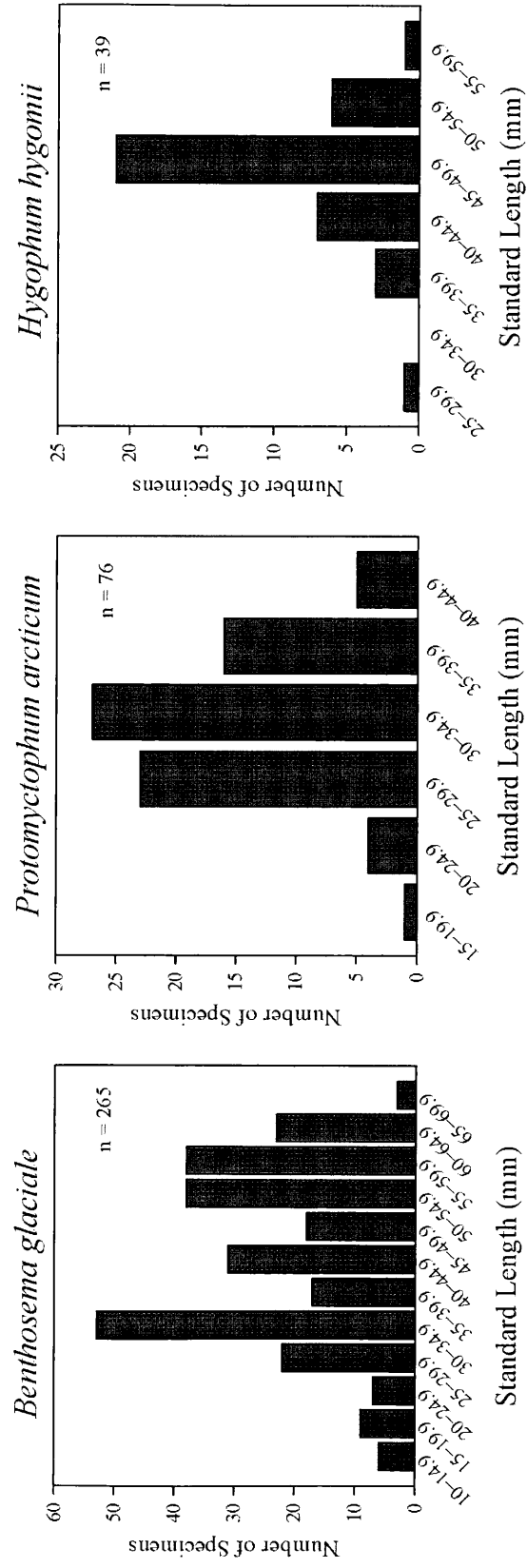


Figure 2. Standard length (mm) frequency histograms for myctophids included in this study. n is the number of each species dissected.

Figure 3. Cluster diagram (A) and scree plot (B) for *Benthosema glaciale*. The cluster diagram represents the relationships among the diet compositions of 5 mm size classes of *B. glaciale*. The scree plot was used to determine the number of clusters into which the size classes of *B. glaciale* should be grouped.

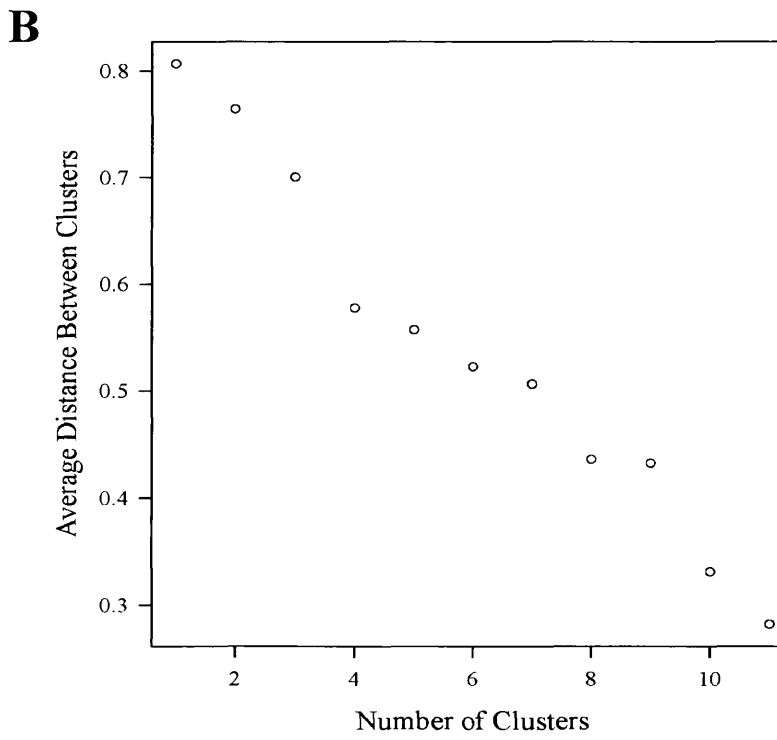
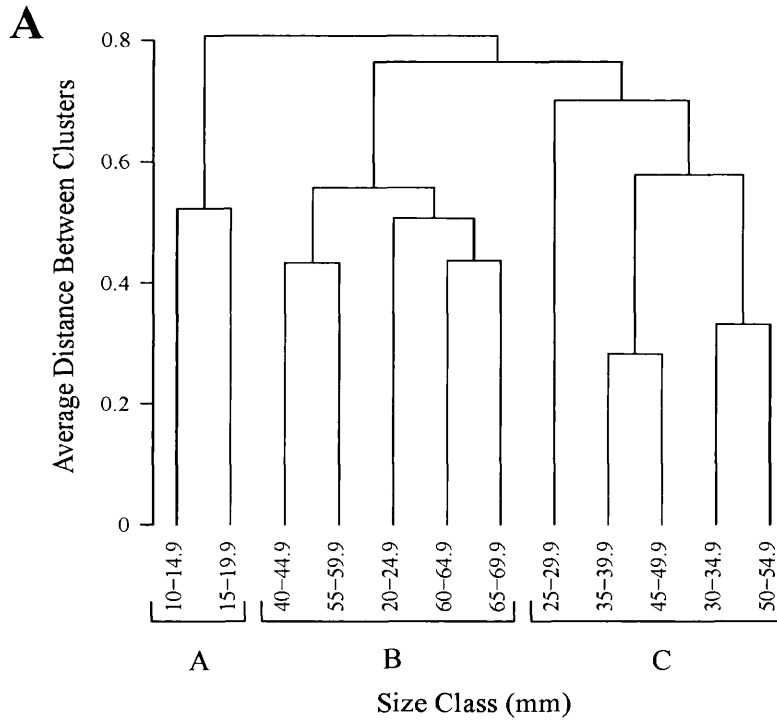


Figure 4. Canonical correspondence analysis biplot for *Benthosema glaciale*. Bolded labels represent the centroids for each level of the ridge section (Reykjanes Ridge, RR; Charlie-Gibbs Fracture Zone, CGFZ; Faraday Seamount Zone, FSZ; Azorean Zone, AZ) time of day, and depth zone (0-200 m, DZ 1; 200-750 m, DZ 2; 750-1500 m, DZ 3) explanatory variables. Points represent prey types in the diet. The canonical axes represent linear combinations of the explanatory variables. Ridge section and time of day were significant at $\alpha = 0.05$.

Benthosema glaciale

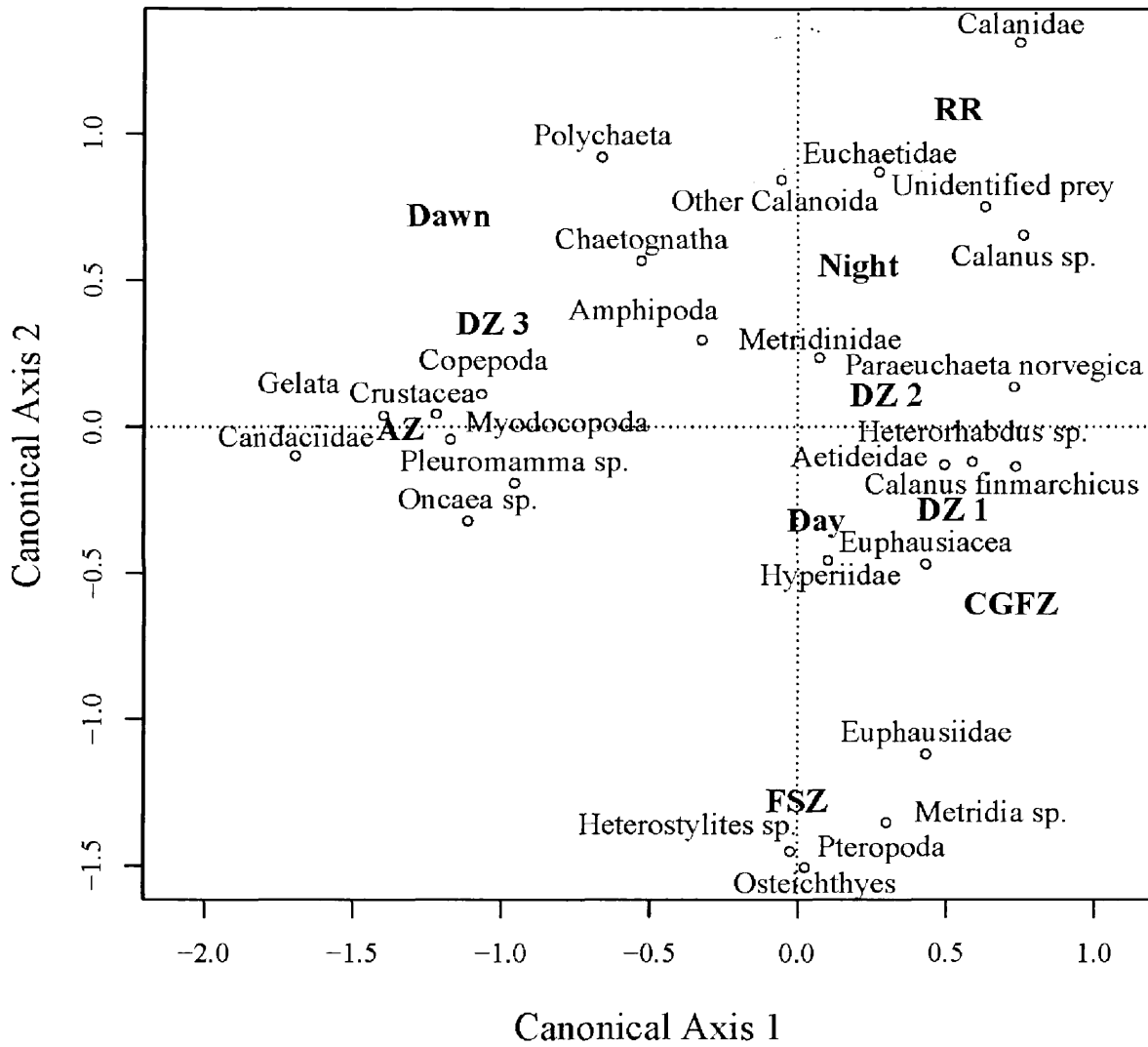
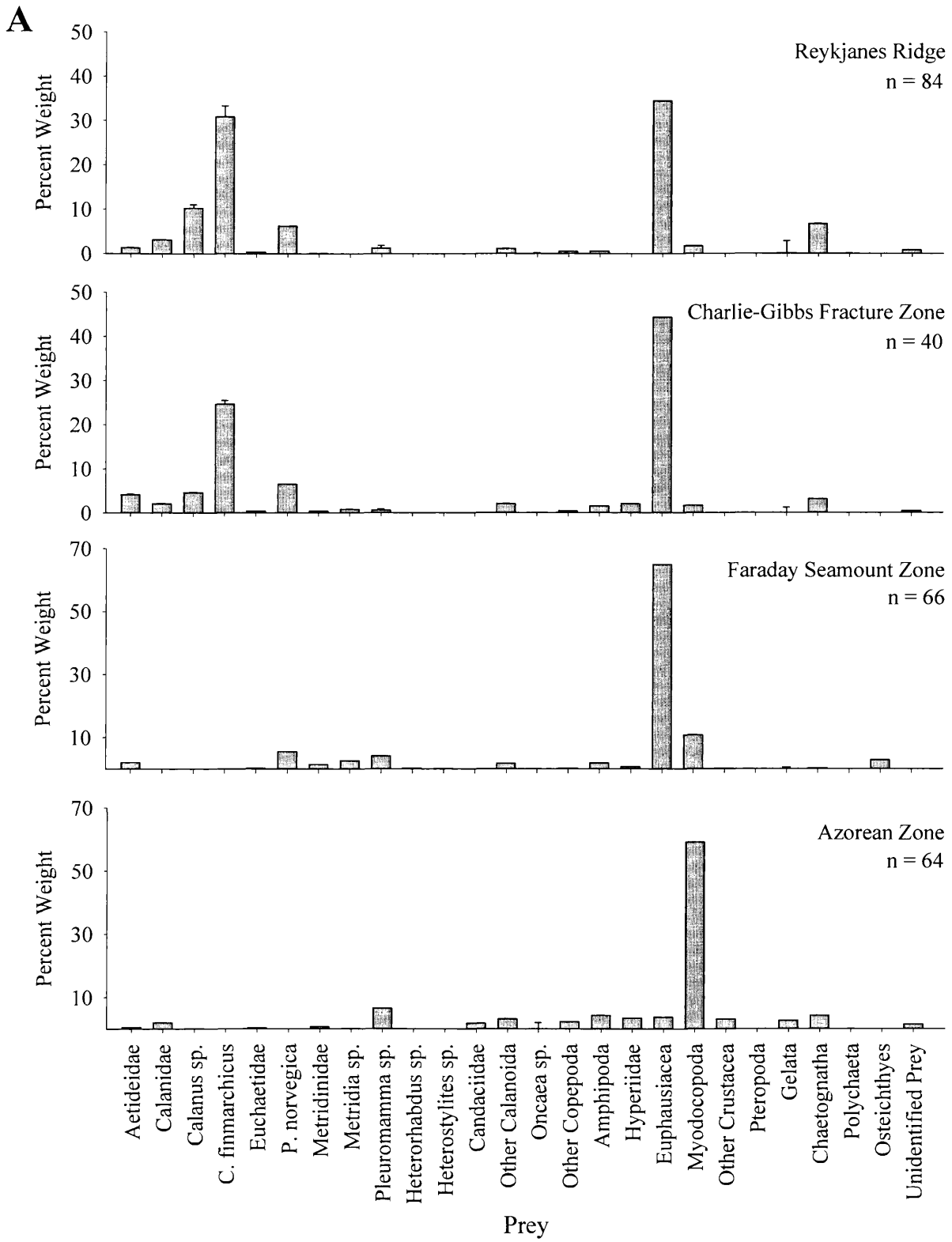


Figure 5. Diet composition (percent weight) of *Benthoosema glaciale* presented by ridge section (A) and time of day (B). Error bars represent standard error of the percent weight values of each prey type in the diet of *B. glaciale*. n is the number of stomachs dissected from each ridge section or time of day. Note differences in scale of y axis for ridge sections and times of day.



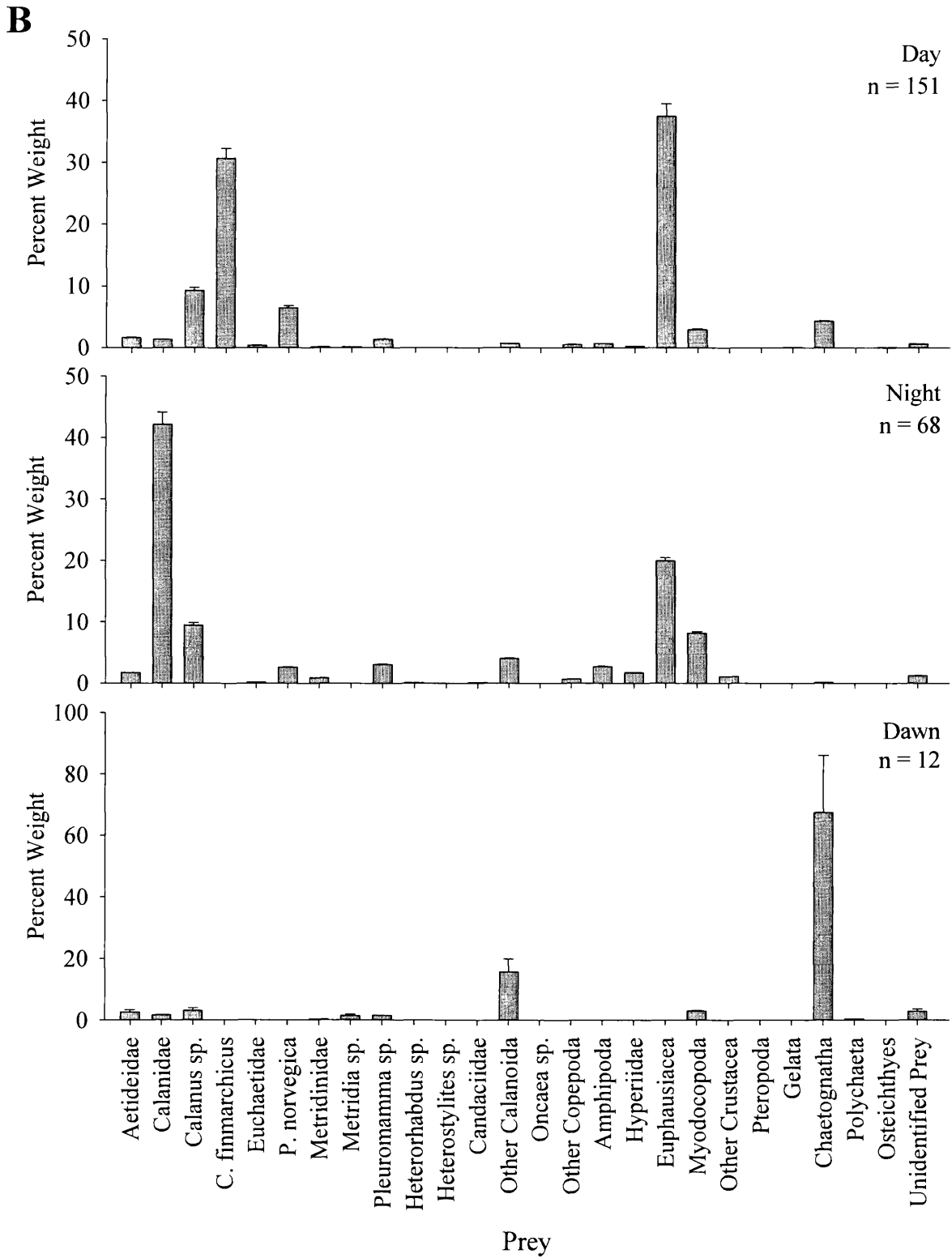


Figure 5. continued

Protomyctophum arcticum

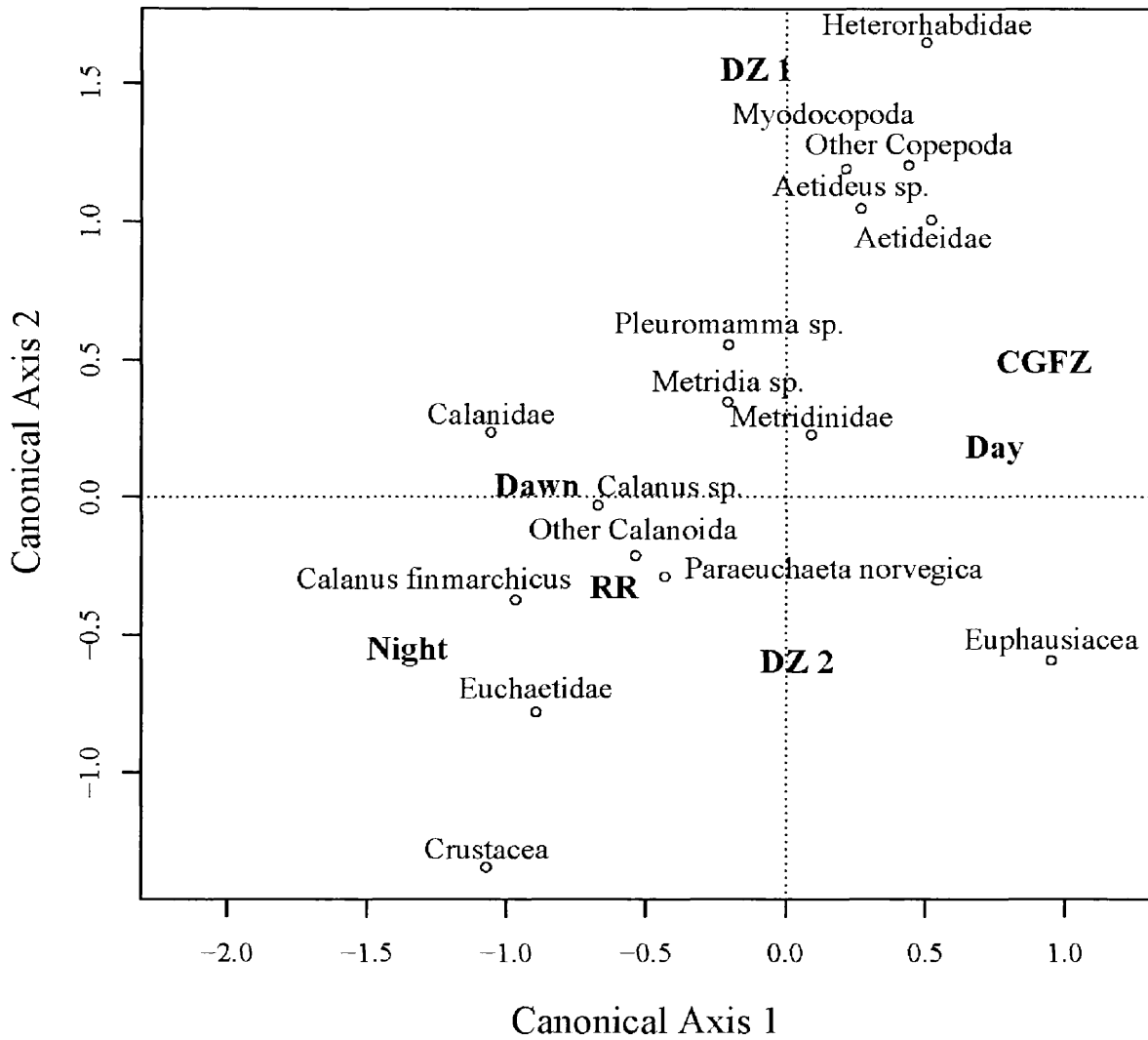


Figure 6. Canonical correspondence analysis biplot for *Protomyctophum arcticum*.

Explanatory variables include ridge section, time of day, and depth zone. Depth zone was significant at $\alpha = 0.05$. For description of explanatory variables see Figure 4.

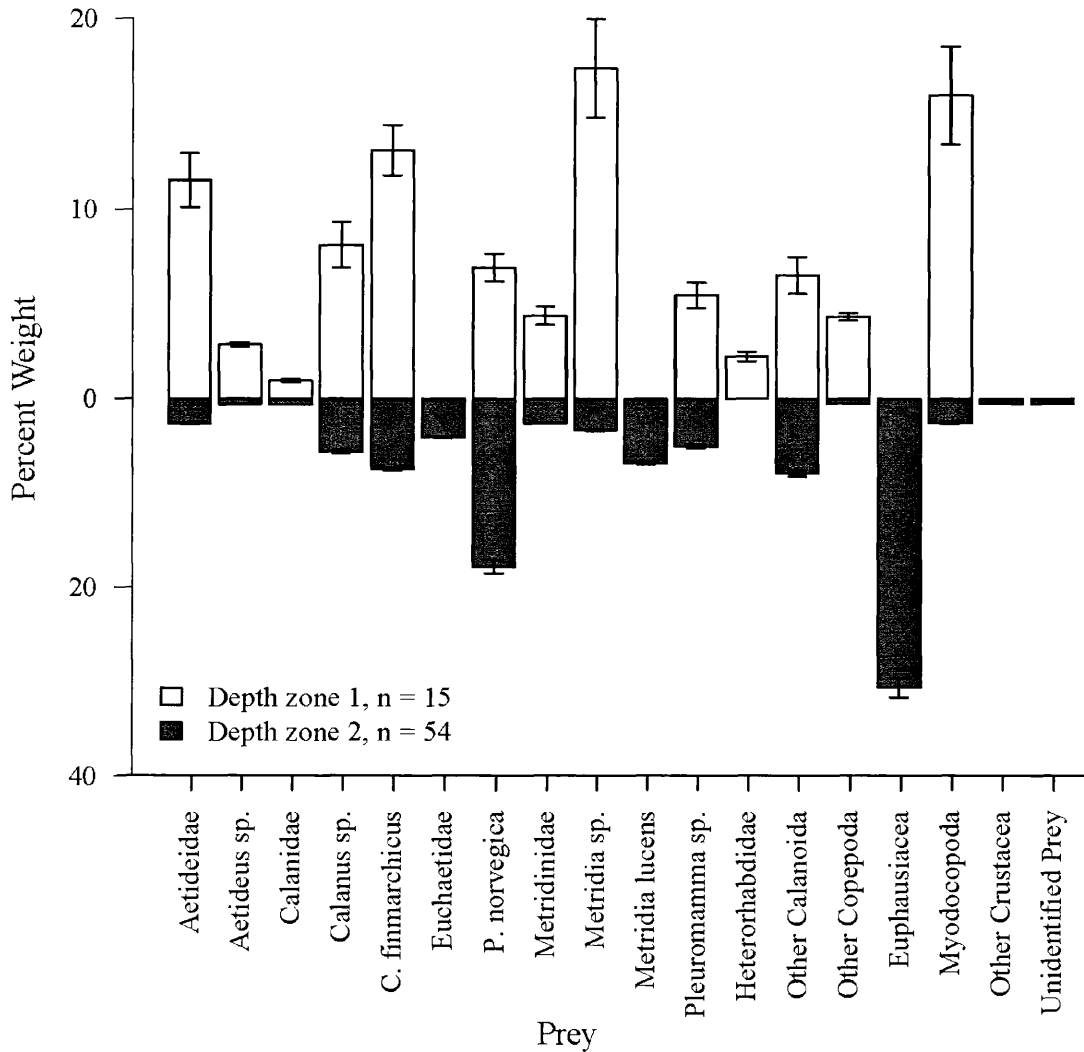
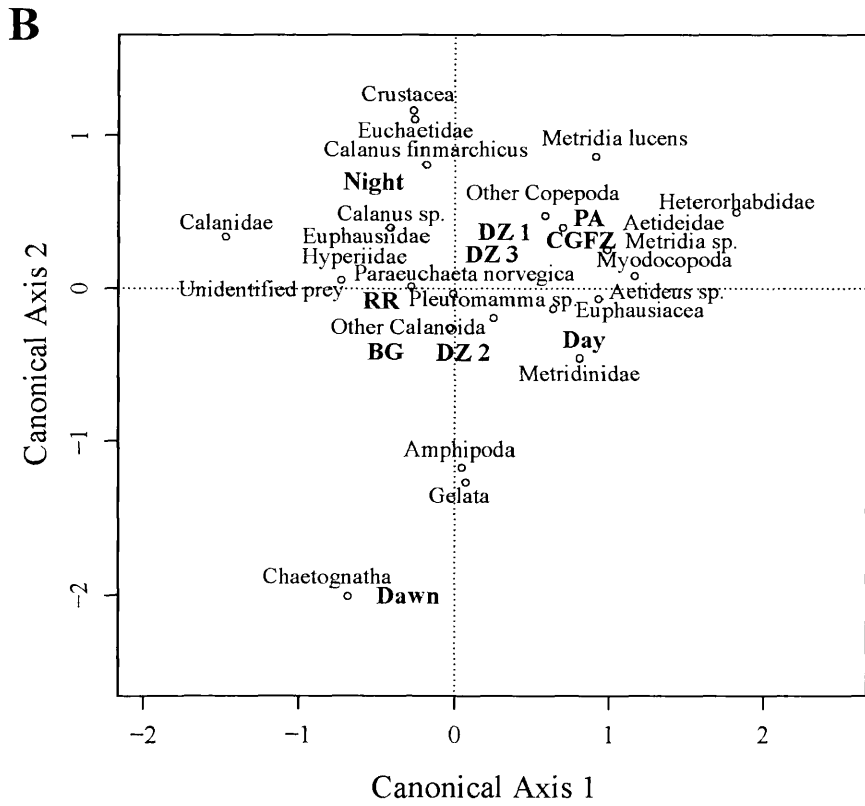
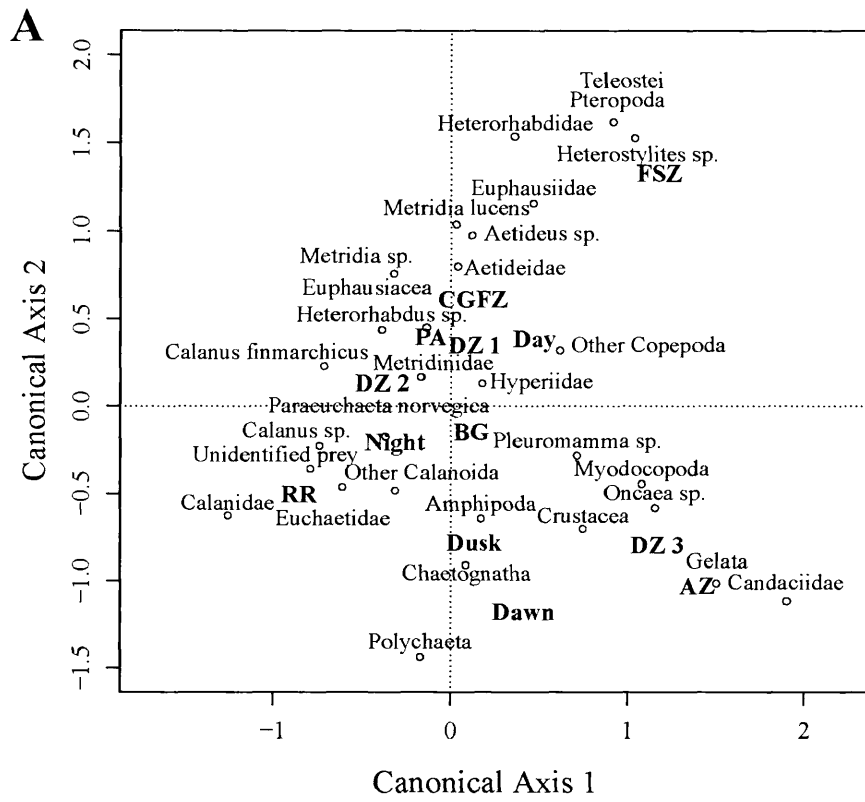


Figure 7. Diet composition (percent weight) of *Protomyctophum arcticum*, presented by depth zone (Depth zone 1, 0-200 m; Depth zone 2, 200-750 m). Error bars represent standard error of the percent weight values of each prey type in the diet of *P. arcticum*. n is the number of stomachs dissected from each depth zone. Note differences in scale of y axis for depth zones 1 and 2.

Figure 8. Canonical correspondence analysis biplot for *Benthoosema glaciale* (BG) and *Protomyctophum arcticum* (PA). A) includes all samples of each species. Ridge section and fish species were significant at $\alpha = 0.05$. B) includes only samples of each species that were caught simultaneously. Fish species was significant at $\alpha = 0.05$, time of day approached significance ($p = 0.08$). Explanatory variables include fish species, ridge section, time of day, and depth zone. For description of explanatory variables see Figure 4.



Vita
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Born August 24, 1986 in Alexandria, VA. Graduated from Culpeper High School in 2004. Earned a B.S. in Biology and a minor in Chemistry from Christopher Newport University in 2008. Worked as a research assistant with graduate student Lance Gardner, Center for Coastal Resource Management, and Virginia Sea Grant at the Virginia Institute of Marine Science (VIMS). Entered the Master's program in Fisheries Science at VIMS in 2009 under Dr. Tracey Sutton, and completed the program under co-advisors Drs. John Graves and Deborah Steinberg.